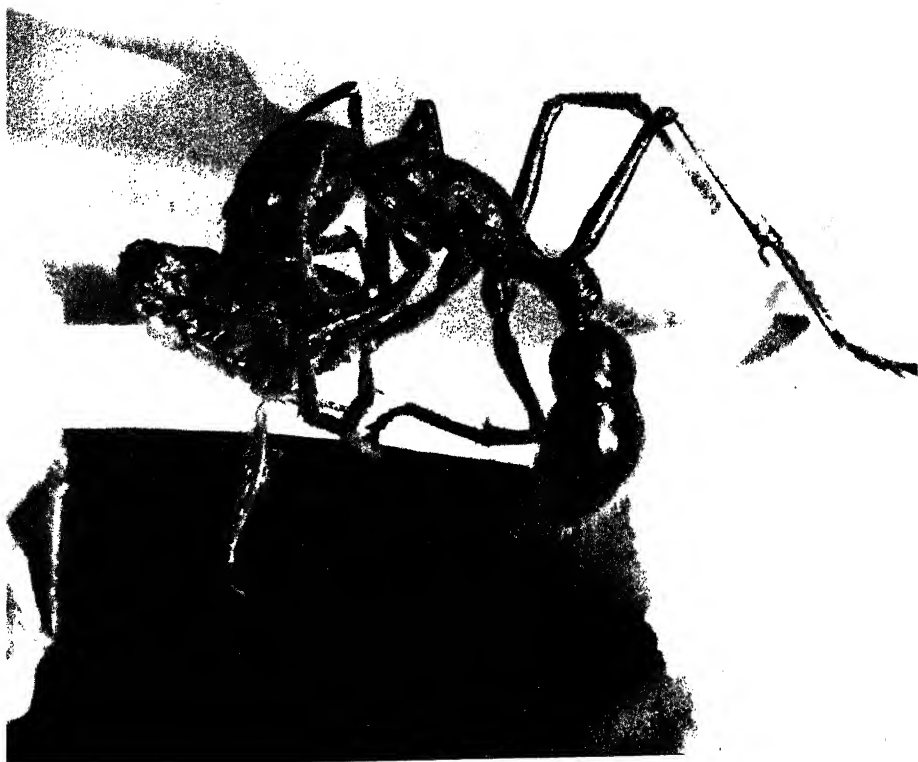


Of Ants and Men



THE KILL

A hunting worker of the giant *Paraponera* has captured a cockroach in the flower of an orchid, and prepares to return home with it. (Photo by D. M. Gallagher.)

Of Ants and Men

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Preface

OBSERVATION of the social lives of ants has long been a fascinating diversion with the author. It seemed, ultimately, that a popular book about certain phases of ant life that had particularly interested him might interest other laymen as well. Long acquaintanceship with living ants leads strongly to the feeling that in the superficial parallels between their social lives and those of men there may lie a somewhat deeper and more fundamental significance than we commonly realize. An attempt is made in this book to point out some of the more obvious of these analogies and to suggest bits of evidence and trends of thought in connection with them.

The author is especially indebted to Mr. D. M. Gallagher and Dr. Paul A. Zahl for many of the photographs which have been included in the book, and to Mrs. Gallagher for complete reading and correction of the proof.

C. P. H.

Schenectady, N. Y.

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INTRODUCTION

Earth Dwellers

SINCE THE DAWN of earliest recorded time, and no doubt far into the misty, uncharted depths beyond, ants have held a fascination for men that has been almost uncanny. No other organism of comparable size, unless it has been of outstanding economic benefit or harm to the human race, has ever engaged its attention so consistently. None but the family of bees and wasps and ants has ever so much excited the philosophic observation and speculation of thoughtful men of all times; and within that family, the ants are easily predominant.

The underlying reasons for this feeling of communal interest, so strong as to amount almost to a kinship, which outstanding philosophic minds have felt for ants in all ages of human development, are certainly many and deep. They form a complex structure only bits of which are evident to us today, but which certainly reflect most important light upon the structure of human society itself.

The immediate reasons have varied widely with the time and the cultural level of the observer. He might

have been a Liberian, whose interest in ants took the form almost wholly of a gastronomic one—whose concern in the colonies of *Carebara vidua* was confined to their gigantic fat queens, which, roasted on the day of their marriage flight, immensely pleased his palate. Further to the south, in the lower half of equatorial Africa, men of Hottentot-Bushman stock felt an interest equal in intensity and practicality, but opposite in kind, in the ever-hungry driver ants, whose perpetually ravenous raiding swarms systematically invaded their camp sites and made other refuges both safer and more pleasant. Men who dwelt in somewhat more complex societies, and whose own superiority in craft and whose greater perceptiveness entitled them to the hard-won title of witch doctor, early sought out ants for the alkaloid-containing poison glands of the sting and the long and recurved mandibles of certain types, which might serve as sutures and ligatures in the binding of open wounds. Such interests in ants, however, are by their nature superficial, relatively primitive, and highly unstable. They are no different from other types of concern displayed by men the world over for features of an economically favorable or adverse environment, and they give to the ants only the dubious honor of being so dominant in an environment that they can affect it to such a degree as seriously to concern a very much larger, more powerful, and more widely perceptive rival.

Wholly different in kind, and with infinitely greater promise of future intellectual joy and satisfaction for the human race, is the philosophical interest in ant societies, and the recognition, which appeared not much later on the stage of human progress, of their indubitable parallelism with the societies of men. In a New World

culture far more primitive than that in which Solomon dwelt there came into being a less-well-known story of the prowess of the ant, of equal significance in a study of the civilization that originated it. Born in the Valley of Anahuac, fathered by some unknown ethnic group of pre-Mexico, perhaps of Mayan affiliation, and persisting into the times of the Conquest, it is inadequately rendered into sixteenth-century Spanish as the *Leyenda de los dos Soles*. It describes the part played by the historic worker of a grain-harvesting ant of the Mexican desert, possibly one of the species of *Pogonomyrmex* or *Ischnomyrmex*, which are common there today, in planting the seed from which, after long and indirect growth processes, both mankind and his environment were developed.

It is just such a linkage of aspects of the social life of ants and of mankind which has prompted much of the best and worst of the more purely scientific investigations of ant societies of recent times. Emerging from the mass of inaccurately presented and ill-digested information and vague, far-reaching, and often unjustifiable imputations which characterize the early literature on ants and the relationships of their societies to those of men, work such as that of Huber and Lubbock and Fabre stood in sharp contrast to the general philosophic trend of the middle of the last century. It laid the foundation for a more complete and infinitely more genuinely appreciative view of ant societies than mankind had ever known before. The studies of these men were for the most part purely observational in character, and based on a knowledge of relatively few and local types of ants. They were necessarily, therefore, of somewhat limited scope and viewpoint on all fronts,

yet the material upon which any philosophic implication was based was accurately and carefully gathered, and a virtually new tradition established. Necessarily, however, any comprehensive comparisons of the societies of ants and men had to wait upon a knowledge of the ants themselves in many parts of the world and under many environmental conditions. A foundation of accurate taxonomy had first to be gathered, and it was necessary that with it should be joined an enormous volume of habit notes, observations of activity under natural conditions, and more extensive and careful studies of the individual behavior of the more reactive ants in artificially controlled environments. The researches of Adlerz and Handlirsch, and of Janet and Mayr and their colleagues and assistants laid the foundations upon which could be erected, during the last half of the nineteenth century, the splendid and extensive studies of Emery, and, best of all, of Forel. Forel, with his *Fourmis de la Suisse* written at the very beginning of his own active life, initiated half a century of intense investigations both of the taxonomy and of the social life of ants. Last and greatest of all outstanding students of ants has been Wheeler, whose broad interests and intensely investigative outlook, at once both warmly human and accurately scientific, have left no phase of Myrmecology untouched. Thanks largely to him, the taxonomy of the ants of the world is now nearly completed, and light has been shed upon phases of their behavior, habits, colonial structure, and activities which were not even suspected at the beginning of Wheeler's work. New truths have been revealed and new views of ant societies necessitated—views both more and less sensational than those which were earlier held. The time at last seems ripe

when, with an adequate background of knowledge of the taxonomy, the distribution, the colonial structures, the evolution, the psychology, and the physiology of ants, we can intelligently ask, and intelligently answer the following questions: Why should we; who are beset with the intricate problems of warfare, sustenance, the relative rights of groups, and a continuing safe existence in a rapidly changing world—problems which, however remotely derived they may be, are rooted in the primal needs of individual and colonial preservation and perpetuation—interest ourselves in the social problems of ants, and the way in which these insects have faced them? Are there any real parallels to be drawn between the societies of ants and men? Can we as we gaze at the ant colony, discern any social pitfalls which menace both groups alike, into which ants, perhaps, have fallen more deeply than men, and from the spectacle of which we can draw a picture in somewhat greater perspective of the social tendencies of our own and other times? To what extent can we “humanize” ant societies without falling into the criminal error of hopeless anthropomorphism? To what extent can we really “go to the ant” for information and help, as Solomon advised, without reading into the structure of ants and ant societies many things that are not there? Have ants, by virtue of their enormously great antiquity as social animals, gained more social wisdom than we humans, and have they fallen into and rectified social errors which we have not yet committed, or have only begun to commit? It is in elucidation of these and similarly fascinating problems, whose correct answers must demand a combination of boldness and caution in concept, which only some exceptionally gifted worker will achieve, that this book is devoted.

CHAPTER I

The Dawn

“AND IN THE BEGINNING, to this land came Arjuna, and by him were the hills and the valleys, the lakes and the cataracts made, and from him have come all our people.” So do innumerable similar tales begin, told in palaces and by open hearths, by medicine men and prophets, among savages and highly civilized folk, whenever mankind essays the fascinating question of its own coming. The question of the origin of mankind and of civilization is one which fascinates and concerns us deeply, and in which very general interest has long been centered. Modern anthropologists and sociologists, armed with the fruits of the accumulated research of more than a century of work, should be able to give us a fairly clear physiological and ethnic picture of the rise of mankind as a social animal, and to point out in reasonable detail the environments and the forces that accompanied the change of humans from solitary to highly socialized beings. Yet when we examine the evidence extant of the rise of societies of men, two surprising facts stand out very clearly. The first is the

incredible meagerness of our information, the second, the youth of our apparently stabilized civilized race. Both these factors are serious disadvantages in the study of man as a social animal. The former necessitates an enormous number of precarious guesses concerning man's ancestors and man's earlier condition, while the plasticity of our present civilization leaves many developments of society half finished, with no good predictions possible.

There are no truly intermediate types now living among men to help us in our search for evidence as to how men lived when social life, with all its implications, really dawned. Our lowest living civilizations, such as those of the Indian Veddahs and the Australian Bushmen, are already far advanced—even beyond the point of the discovery of fire—and are essentially like our own. The finished product has been formed, and the mold by which it was made has been forever destroyed.

We are forced to depend wholly upon paleontological evidence, and it is pitifully scant. Here and there a jaw bone or a skull, a thigh bone or some vertebræ tell a mute, abbreviated story of man's change to his present form, but are silent on the most important part of all—the social instincts, the real life that he led. Java yielded such fragments in 1891 to Dr. Eugene Dubois, a Dutch army surgeon—fragments of a skull with the characteristics of the primitive gibbons, but associated with teeth intermediate in form between those of apes and men, and with a thigh bone which is definitely human. *Pithecanthropus erectus*, the erect ape-man, does seem to have been intermediate between the apes and men. But of the warp of his life the rocks—of Middle Pleistocene time—are wholly silent. Far more tantalizing are the

remains of a much more manlike creature, *Homo neanderthalis*, the first evidence of which was discovered as early as 1856. Stone implements, the first marks of civilization, were found in association with the remains. What had happened in the years between the appearance of the ape-man and the Neanderthal man?

We know nothing whatever of all this. Suffice it to say that whatever changes occurred came with extreme rapidity, as evolution goes, for the total fossil record of man's ancestry represents probably no more than a million years of the history of our earth. Yet it embraces the appearance of *Pithecantropus*, of the Neanderthal man, of the Rhodesian man, of the magnificent Cro-Magnon man of high forehead and commanding mien, whose cranial capacity exceeded our own, and of modern man. This short time must have witnessed the completion of the physical changes involved in the assuming of an erect posture, the development of the brain cavity, the shortening and reduction of the face, and the increasing physical weakness of the individual, which accompanies advancing civilization. Much more significant, it must embrace the whole rise of society, from its most primitive family configuration to the greatest national and international consociations of all times. It must at once include a forest creature anxious to defend a mate and single child, a primitive head-man of a half-formed tribe, and the most highly developed of international thinkers. And of all the details of this development, save the very last and least significant part of it, we must remain completely ignorant.

We must remain completely ignorant except by the analogy of other organisms about us, whose social development has been carried out in the same world and

under the same conditions as our own. There are but few living creatures whose social development at all parallels our own, and among these the ants are predominant. We shall see this, although the growth of social institutions among ants has often followed a course far different from that of men. Nature has ultimately forced both to the same mold. A comparative study of the two serves to emphasize the mold in bold relief, to reconstruct some outlines of our unknown past, and to aid speculation as to our unknown future.

When we examine the evidence available for the social evolution of the ants, we find a wholly different picture from that which obtains among men. Here we deal with a race of enormously greater antiquity. In the very earliest of Tertiary times, separated from our day by fifty million years or more, the social life of ants had almost ceased evolving, and their final physical form was almost fixed. At a time when the most primitive of placental mammals occupied the center of the stage of the warm-blooded four-footed creatures, ants were so much like their descendants of today that some of them, as fossils, can actually be assigned to living genera. Throughout the entire time that mammals have gone through their momentous evolution, which has culminated in the primates and in the development of men, ants have had the opportunity to appreciate and cultivate the nuances and the fine advancements and degeneracies of social existence—to experience hazards of organization and perils of development of which mankind is only today becoming aware. What an immensity of social wisdom, though not of mental wisdom, that archaism can afford we shall later see.

Yet ancient as are the ants as a group, and highly

socially specialized as they have become through their long evolution, they have continually thrown off primitive, arrested forms that have survived to the present day, to a degree unprecedented among men. So many of them exist in the world today—although, for the most part, as timid, unobtrusive societies of great rarity—that from an observation of them we can construct a picture of the social evolution of ants that is infinitely more complete in its details than any comparable picture of mankind. And in addition, fossil records are available which are so complete and beautiful that wandering worker ants which were trapped in the sticky resin of the ancient Samlandic black conifer forests of Germany and Central Europe two million years ago are more perfectly preserved for us today than are the sentries of Pompeii and Herculaneum. Their very guests and parasites, the co-dwellers of their home nests, are preserved with them for all time.

From studies of such fossil records, from a consideration of the distribution of the ants of today and from a study of the structure of the social groups which now survive, we can construct a picture of the rise and growth of ant societies which far eclipses in its perfection the story as we know it for man. It is to a survey of the general character of this evolution, and to a consideration of its similarities to and its differences from that of man that this chapter will be devoted.

The Hymenoptera, or group of stinging insects to which belong the ants, bees, wasps, and various solitary forms, apparently arose in Mesozoic time, fifty to one hundred million years ago. It was the time when the dog-toothed reptiles were first giving rise to the warm-blooded mammals, and when the dinosaurs dominated

the world of the vertebrates. These Hymenopterous insects had apparently been derived from cockroach-like creatures, the most primitive of insects, themselves arising from more primitive jointed animals, the ancestry of which is in turn traceable to the worms. Like their cockroach ancestors, the first Hymenoptera were apparently solitary insects, with coarse, longitudinally-veined wings carrying but few cross-struts to strengthen them, only imperfectly adapted for flight. Like the first birds and the cockroaches of today, flight was probably somewhat precarious for them, and may have been indulged in but seldom. Gradually, however, body specialization and flight perfection progressed, and by Jurassic times there existed races of winged sawflies, not unlike those of the present day except in size, although definitely more generalized. Fossils of these from the Lower Purbecks of Durdlestone Bay, in England, were described in 1854 by Westwood and have been found still better preserved in the Solnhofen limestone of Bavaria.

If we may judge from the behavior of the sawflies of the present day, these ancient creatures were accustomed to lay their eggs in incisions of the bark and surface wood of the primitive trees amid which they lived, and the young, hatching in these situations long after the death of the mother, fed on the woody tissue of the plant until maturity was achieved. It was but a short step from such a development for the mother insect to deposit her eggs upon the bodies of living animals instead of plants, and for the larvæ, upon their hatching, to burrow into the tissues of their host. So, apparently, arose the groups of parasitic Hymenoptera, which still persist today in the ichneumon flies, and from

which there is little doubt that the ants, the bees, and the solitary and social wasps are descended.

Some of the members of this parasitic group perfected their habit of internal preying. Their adults became amazingly acute in locating the host of a particularly desired species, and they learned to implant their eggs in positions and in numbers which would insure the maximum survival of the coming generation. Such forms are with us today, and constitute the most interesting of the parasitic Hymenoptera. They represented an evolutionary blind alley, however. Their relationship to the ants is perhaps analogous to that of the Neanderthal man to modern man. It was not from them that the ants were to be derived.

Other parasitic, wasp-like insects took another course to perfect their relationship to their prey. Instead of seeking it merely to deposit their eggs upon it, and to leave the eggs to the ministrations of a highly uncertain Fate, the mothers belonging to this group undertook to sting and at first to kill, later only to paralyze, the prey before an egg was placed upon it. Finally the habit was developed of building a special clay cell to protect the paralyzed prey, and to keep the developing larva out of sight until its growth was completed, long after the death of the mother. This more "intellectual" group, in which a far greater degree of responsibility for the safety of the young was assumed by the parent, survives today in the solitary wasps, represented by every steel-blue "mud-dauber" that hovers over puddles in a country lane of a sultry summer's day. They are of the line from which the ants were to be evolved.

The primitive solitary wasps were all, or nearly all, carnivorous, and they all possessed the attribute of

parthenogenesis, which they have retained to this day, and which all their descendants, including the ants and bees, fully share. Males are unnecessary to the production of young, although, in general, unfertilized eggs will give rise to males, fertilized to females. These traits the early wasps retained in common, but in less fundamental habits they soon became highly diversified. Some took increasingly to the air, and evolved swift-flying hawk-like forms of great size and beauty. Others became much more terrestrial, and lived and hunted within the earth, the size of their eyes becoming reduced accordingly, and the use of their wings much restricted. The swift-winged members of the family were destined to give rise to the modern wasps and bees. Our interest lies with those slower, more deliberate, more realistically humble forms, which turned ever closer to the earth, and from which, with little doubt, the ants descended.

Insects of just this type are represented alive today, in many parts of the earth, in the family *Scoliidae* of the Hymenoptera. They are very ant-like creatures, small and inconspicuous, living myopic existences in the close-packed darkness of leaf-mold and fern-root. Many of them are easily found in the pine needles and black earth on the floors of shady northern forests. Both male and female are winged, but the female uses her wings but little, and is strongly reminiscent of a primitive ant in her general appearance. She is wholly carnivorous in habit, and lays her eggs in the soil, where her young develop. She dies long before their maturity.

What may be the causes of an increase of the life-span of an organism we cannot, at this stage of our knowledge, adequately guess. Possibly the causes which brought about an increase in the span of life in the early primates

and in man over more primitive mammals were also those which produced a gradual increase in the length of life in the females of some of the Scoliids. A decrease in physical activity, with the corresponding decrease of metabolic wear and tear, or the seeking of environments having a limited oxygen supply, may have been partly responsible. In any case, the situations are strikingly parallel, for there is almost no doubt that, in one branch of the Scoliids, the life of the female gradually came to be prolonged so that it overlapped the hatching of her young, and a very primitive sort of family life forthwith developed. The actual transition from the completely solitary to the subsocial stage of life is represented on earth today among the bees and wasps, but not among the ants, whose great archaism seems to have resulted in the loss among living forms of this one stage of the process. However, every ant queen, in founding her colony today, reviews this process of social evolution, although, among the higher ants, certain secondary developments have obscured the picture. When some future student shall have discovered the details by which the queens of the great primitive ants of the tropical jungles found their colonies, we should have the drama reenacted before our eyes in almost its exact entirety.

It seems clear, from the evidence of the behavior of bees and subsocial wasps in their colony foundation, and from the fragmentary knowledge which we now have of the behavior of the young females of very primitive ants, that the young Scoliid female gradually came to take a thoroughly maternal interest in her brood, whose life hers now overlapped. She began to forage for them during their growth, instead of merely provisioning

them once and for all with a huge paralyzed body of her prey at the time that her eggs were laid. At first she must have died long before the helpless young were grown, and probably she compensated for this by leaving a great excess of food available at the time of her death. But eventually the life of the mother was extended so that she survived the complete growth of her young, and was able to provision them at intervals throughout their development, remaining near them to protect them the while.

Thus was the first great stage in the evolution of the social life of ants completed. Its final product is the picture of an aged mother with her grown brood of young. The next step was equally momentous to the development of a successful social organization. For reasons which we today cannot adequately fathom, but in the operation of which we can see numerous parallels throughout the kingdom of animal life, the newly matured young insects came by preference to remain together, and with the mother, so that the little family group constituted an organization not unlike that of a covey of quail. The entire structure of the social organization of ants has been built upon the ever-increasing stability of this group—a stability brought about by forces strikingly parallel in their action to those governing human social development, but at present unknown to us. The longevity of the mother gradually further increased, and the dependence of certain of the young upon her increased also. Strikingly enough, this development was wholly restricted to the female sex. The males of all ants remain to this day primitive, nonsocial organisms, closely comparable to their Scoliid ancestors, and in many cases scarcely distinguishable therefrom.

Physical degeneration soon occurred among certain of the female progeny of the original mother, leading to a reduction of fertility, loss of body size, complete loss of wings, and other specializations. The causes, or even the attendant body and germinal changes, of this momentous transformation are completely unknown today, and their investigation might throw much light upon our knowledge of the development of social organisms in general. Social evolution, like evolution of every other sort, seems to progress by rapid, unstable jumps, alternating with periods of relative stability. The evolutionary stage in which the loss of wings, some stature, and complete solitary autonomy by a portion of the daughter insects took place was apparently a transitory one. For no living sign remains on earth today of the primitive Scoliid-like mother with her group of independent, winged daughters whose maturity she survives, but which soon scatter, leaving her alone to die. Yet of the stages on both sides of this transition we have innumerable examples. We have already seen that there are abundant living Scoliids which are earth-dwelling, carnivorous, parthenogenetic, and thoroughly ant-like, but among which the mother never survives the hatching of the young, and which are, in consequence, wholly solitary. On the other hand, there are to be found alive today, under very special conditions, many forms in which the wasp-like mother survives the maturity of her daughters, but these, although very closely resembling her, have already lost their wings, and suffered at least a slight reduction in fertility. They are still carnivorous, earth-dwelling, parthenogenetic, and otherwise unchanged, yet the transitional form, by which they were derived from

their still-living ancestral forms, has as completely disappeared as though it had never been. Perhaps some future explorer shall discover it in a little-known corner of the Old World tropical jungles.

This semisocial Scoliid group represents the very beginning of the true ants. With some types more highly specialized in certain peculiar features, but still extremely generalized as a whole, they are placed in the subfamily *Ponerinae*, comprising the ancestral stirp of all ants, the group in which the social life of ants is seen in its simplest and most primitive forms. In many respects, this is the most fascinating group of ants for the sociologist, for it parallels, to an amazing degree, the Neanderthalic stage of human progress, yet is alive today in many parts of the world, so that its social structure may be studied in detail.

We are as ignorant of the localities in which the transformation of the solitary Scoliids to the subsocial ants took place, and of the hub of distribution for ants over the globe, as we are of the origin and distribution center for modern or ancient man. It is not at all improbable that the transition from a solitary to a social existence among ants may have taken place a number of times among races not directly related. This may have led to the nearly simultaneous production of several races of ants only distantly related, comparable to the six or seven independently evolved races of men which must once have existed. But unlike mankind, many of these ant races have been preserved side by side to the present day. No one of them has succeeded in exterminating the rest, although all have retreated like forest gnomes before the onslaughts of more modern types, as we shall presently see.

There is much indication that during Mesozoic times extensive land bridges existed between the present-day continents of Eurasia, Africa, Australia, and the Americas. This entire area, apparently, was inhabited by a primitive, cosmopolitan, widely distributed group of Ponerine ants, at that time the dominant insects, and for the most part of large size, although their daughter workers were already wingless. Ponerine ants occur even in New Zealand, which has been isolated from its mother continent ever since Jurassic time, a hundred million years ago—the epoch when the first primitive birds were making their appearance. In Australia, and in isolated portions of the tropical jungles of both hemispheres, groups of the giant Ponerines still exist, resembling great wingless terrestrial wasps, with large eyes, huge mandibles, and great stings. A study of their social habits, as we shall see in another chapter, clearly reveals the origin of many of the highly complex social customs of the higher ants.

There is evidence that long before the close of the Mesozoic era, the primitive Ponerine ant fauna had split into several very distinct lines, in all of which the colony life had become increasingly stabilized, and the numbers of individuals composing the colony much augmented. The life-span of the queen steadily increased, while the dependency of her daughters upon her became much more marked, and extreme social differentiation took place. Even among the more modern Ponerines of today we find greatly intensified specialization in the worker caste and an increase in colony size from a dozen fugitive young leading relatively solitary lives to several hundred well-defined workers whose hunting, raiding, and colonial life is carried out much more in concert.

There are existing Ponerine ants which habitually live roving lives, continually pillaging and looting in company to supply the living food that the colony demands. So it is not surprising to find that, from some branch of this sort, a stem separated from which was to be developed a group of ants representing today one of the most striking features of the New and Old World tropics—the driver or legionary ants, the *Dorylinæ*. While still retaining their primitive carnivorous habits and for the most part their generalized body organization and limited intellect, this type of ant swelled the numbers of its colonial family from a few dozen to many thousands. Differentiation among the daughter workers into soldiers and many grades of workers took place. Relationships between members of the colony necessarily came to be enormously complex, to keep pace with the increased population. Since the primitively carnivorous habits were retained, it was necessary for the colony to be forever on the move, to continually appease its ravenous appetites. So this group of exalted Ponerines, the Dorylines, came to wander continually, bivouacing only for a few days in any one locality, ever rapacious, ever fiercely striving to satisfy a well-nigh unappeasable hunger. The tremendous increase of colony numbers, without correspondingly significant increase of physical adaptability or intellectual plasticity, has produced a very unstable condition, and only the unremitting effort of all members of the huge organization can save it from dissolution. Such effort is fruitful, however, for many species of the Dorylines are conspicuous features of the tropical scene, both in Africa and in South America, where their frequent raids on human dwellings cause them to be well known. Spectacular they are, but

fundamentally they represent no more than a much-overdeveloped branch of the Ponerine ant family, no more than the overdeveloped societies—at once highly artificial and fundamentally completely savage—which have played a prominent part throughout the history of mankind. Since the sub-family *Dorylinæ* occurs in an almost equally high stage of specialization in Africa and America, it seems highly probable that the main lines of its evolution were well advanced before the separation of those continents, which occurred during Eocene times.

During the Mesozoic millenia, while a branch of the Ponerines was thus building a complex form of social organization on a thoroughly insecure foundation of individual endowment, another branch was developing quite differently. This group long retained its modest status as a small, self-contained family, but underwent a number of individual changes, which proved fundamental to a really permanent advance. Some of these changes were physical ones. . The physical gap between the queen-mother and her first daughters was widened, especially in the direction of decreasing stature and strength on the part of the latter. These acquired the ability to come to maturity in the shortest possible time on the least possible amount of food, and thereby to lighten the burden imposed upon their mother in rearing them, both by demanding less food from her, and by greatly shortening their helpless period. They had to make grave concessions, however, in order that this should be possible. They sacrificed physical vigor, and suppressed all the organs that they did not immediately need in the service of their family group. Eyes, legs, and antennæ were completely retained, but even the seg-

ments of the body which should bear wings vanished. Fertility, enjoyed by the workers of the Ponerines, was suppressed, and the life-span of the worker was greatly reduced in comparison to that of the mother. The mother, on her part, underwent a change of behavior in her method of founding the family. Instead of periodically leaving her cell where the helpless young were concealed to forage for them, she became self-contained. When leaving her home colony to found a new one, she descended to earth after completing her marriage flight, analogous to that of the bee, tore off her wings, excavated a single burrow and incarcerated herself within it. Very shortly her wing muscles were broken down and converted to a fatty substance, which was passed to her salivary ducts. This fat, and this alone, nourished the first brood to maturity. The mother herself took no nourishment during the entire process of colony foundation, but as soon as the daughters become mature they broke through the surface of the soil, foraged, and brought food back to the foundress. The queen never left the colony again. This is the method of colony formation practiced by the queens of the vast majority of modern ants today, and, however complex the final structure of an ant society may appear, it can trace its origin to these simple family beginnings.

Certain other modifications likewise occurred in this progressive branch of the Ponerine ants. The exclusively carnivorous diet was abandoned, and a very much wider range of food substances was adopted. Honey, nectar, seeds, plant materials, all came to be regarded as acceptable, although insect food was—and among most modern ants, still is—preferred. Greater breadth of vision came in the selection of nesting sites. No longer

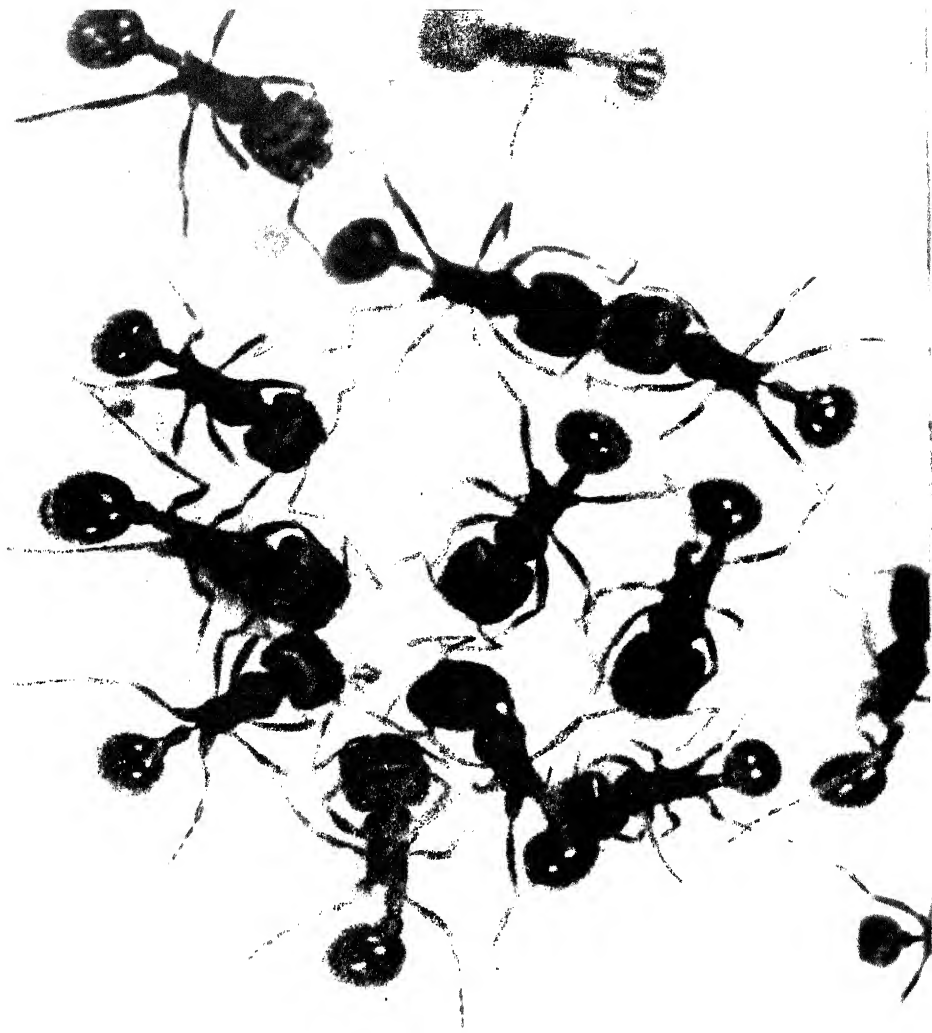
was the soil alone considered suitable as a nesting medium, but decayed wood, the bark and twigs of trees, galls, fruits, and flowers came to be accepted. Several groups actually reverted to the paper and clay building habits of their wasp ancestors, and still practice this sort of architecture today.

These changes, though subtle and relatively inconspicuous, occurring as they did in small family groups, and without much immediate effect on the size or structure of the colony, were actually of enormously greater significance for the social advance of ants than all the showy but inadequate social specialization of the *Dorylines*. In exactly the same way we consider the modest and inconspicuous advance of scientific thought in our own civilization today of greater benefit to it than the much more showy activities of armies and politicians. The specialization of the worker to rapid maturity and short life, coupled with the greater longevity of the queen, paved the way for the development of many generations of daughters during the life of the mother, and permitted her as an adult to outlast the complete adolescent and mature life of many of her daughters. Thus she became a stable entity, a sort of monument to organized society, present at the first coming of all of her daughters, and still present at the death of most of them. Her increased self-dependence, as reflected in her ability to isolate herself completely from her surroundings during the first uncertain days of colony founding, enabled her to survive where her elder, provisioning sister would have perished. A wide range of localities was thus opened to her in which she could found colonies which would have been closed to her predecessors—regions where a mature colony, supplied with many foragers,



THE CARTON NEST

Some ants build nests of paper, very like those of the wasps. This is the paper nest of a species of the Myrmicine genus *Cremastogaster*, dwelling in Indo-China and the Straits Settlements. Such nests are extremely populous. (Singapore. Photo by D. M. Gallagher.)



A HARVESTING ANT

Workers of the harvesting genus *Pogonomyrmex* pause for a sip at a bit of syrup. Notice their great heads, carrying the powerfully built mandibles and mandibular muscles, which they need for crushing and husking seed. (Twin Buttes, Arizona. Photo by D. M. Gallagher.)

could survive, but wherein a single queen, forced to hunt for herself, would soon perish. The diversification of appetites extended this range for the mature colony, and permitted it to survive in parts of the world where animal food is not always obtainable. Far more important than this, it brought ants into the class from which the Dorylines were excluded—the class of herbivorous animals, which alone, as the history of all life indicates, is capable of producing permanently satisfactory social structures.

Once this basis of social development was established, the development of a stable colony structure, culminating in the remarkably complex organizations of ants of the present time, apparently came rather swiftly. The Ponerine stock became differentiated into three principal branches, the specialized representatives of which constitute the great families of modern ants as we know them today. Two of these branches were, to judge by the present geographic distribution of ants, clearly foreshadowed even in that far-away epoch before the separation of the continents. In one of these the sting was retained and agricultural habits were emphasized. It became the subfamily *Myrmicinae*, which, because of its eventual social specialization, we shall later consider in greater detail. The other group, including insects in which the primitive sting was replaced by the formic acid glands, represented the ancestral stirp of the subfamily *Formicinae*, which is the dominant and most conspicuous of modern ant types throughout the world today.

Much later, following the separation of Africa from Eurasia, the Ponerines apparently gave rise to still another group, the *Dolichoderinae*, one of whose members,

the now famous Argentine ant, has but recently undertaken a world conquest which we shall later examine in detail. These ants are of world-wide distribution today, but are a rather quiet group, nowhere especially conspicuous except when, as with the Argentine ant, individual members of the family have undertaken the role of conquistadors.

From the Myrmicine ants have come great agricultural societies of grain harvesters and fungus growers, and members of this group have come to occupy every portion of the globe habitable by man. The Formicine ants have given rise to the slaveholding groups, to many groups which cultivate various types of insects (both habits are likewise known among the *Myrmicinae*), and to the types which are considered most highly developed mentally, as individuals, among ants today. Many of their societies, while actually less conspicuous than those of the driver Dorylines, or of some of the less plastic Myrmicines, are definitely of a higher type in exactly the sense that the society of Athens surpassed that of the Egypt of the Pharaohs.

Such were the beginnings of ant society, shrouded in some mystery, it is true, but to a far lesser degree than is the case with man.

Ant society differs developmentally from that of mankind. It is of far greater antiquity, and it has been able to depend upon a vast host of genera and species to carry it on, whereas the society of man has depended for its furtherance upon a handful of species at most. The first condition has resulted in the establishment of associations far more "finished" today—albeit less intellectually advanced—than those of men, and hence of the greatest philosophic interest. The inevitable conse-

quence of the second condition has been the survival to the present day of a nearly complete evolutionary series of living social forms, including a vast number of "living fossils" and "missing links," whose societies are available for study. A survey of the Ponerine, Doryline, Myrmicine, and Formicine subfamilies of ants, as they exist today, cannot but impress us with the unique opportunity which is ours to pass in review, in its intimate details, the whole picture of the social development of a sister organism of our earth, which, more than any other living creature, has faced the problems of social organization that have beset and perplexed the advance of man. We turn to such a survey in the next chapter.

The Ants of Today

THE BOUNDARIES of genera and species which taxonomic biologists employ are at best pitifully artificial things, crutches with which to attempt to understand the derivation of life. And so it happens, almost inevitably, that any group of animals and plants, which superficially appears a most compact and homogeneous unit, will upon further examination be found to contain the widest diversification in membership. It is so among the Ponerine subfamily of ants. The Ponerine subfamily, admittedly constructed to receive the most primitive of living ants, has had to include among its members the most diverse types whose only common characteristic is their undoubted antiquity. We have no better guarantee that ants originated from a single group of wasps than we have that mankind originated from a single type or source, and so it is highly probable that among the Ponerines we may find representatives of several wasp types that have crossed the border-line into the field which we call that of the ants. Such a hypothesis surely would be helpful in explaining away

the teeming anomalies that await the student, the puzzling cases of parallel and convergent development, the doubtful cases of real consanguinity. We can only say, as we survey the Ponerines, that we are gazing at a cross-section of a typical ant fauna of early Mesozoic time. There are among the Ponerines types which are fully as advanced socially as many Myrmicine or Formicine ants, such as those of the genus *Odontomachus*. But such overlapping is clearly inevitable, and our interest in the Ponerines will lie primarily with the most primitive types living today.

The most generalized and primitive of Ponerines are usually conceded to be those of the genus *Myrmecia*, exclusively inhabiting Australia, where they occupy a position analogous to that of the bushman among humans, the Eucalypts among trees, the "three-eyed" Rhyncocephalic lizard among reptiles or the platypus among mammals. The genus *Myrmecia* includes a large number of species, all of which are rather similar. They are typically very large, active, fierce and conspicuous insects, occupying exposed situations, where they nest in the soil, and even in rotten wood. They are armed with formidable stings and are rather fiercely pugnacious. The workers have large eyes, and are fond of the open. All of these features are almost peculiar to this genus among Ponerines, and represent a definite mark of the sheltered life which they have led. They alone are still boldly dominant over large areas of land, exactly as we believe such ants in general to have been in Mesozoic times. Everywhere else in the world such primitive types have retreated before the advance of more modern civilizations, exactly as have ancient men, and have in general sought refuge in the denser forests and in the

deeper recesses of the soil. A few gigantic Ponerines still persist outside of Australia, and appear dominant, but all of them are confined to the denser tropical jungles of the world. Thus the warriors of *Dinoponera grandis*, the largest ant in the world, still hunt in files in the Amazon jungles, and the closely related and somewhat more widely distributed *Paraponera clavata* still excavates the huge entrances to its crude earthen colonies about the bases of trees through the deeper forests of the American equatorial belt. These ants are formidable to come upon, and still more formidable to capture. They are much feared in their own land, and their colonies are to all appearances impregnable. Yet actually their day has long since waned. They depend for their survival, which may last for only a few more thousands of years, upon the persistence of the stable, protected environments in which they must live. They are unable to increase their range and are as powerless as the physically magnificent Australian bushman to cope with the advanced families of their own race.

The great majority of Ponerines are fugitive types. They are small and inconspicuous, living by suffrance in a modern world, driven nearly or wholly beneath the surface of the soil for their living, eking out a precarious, primitive social life in the very woods and fields whose better parts are preëmpted by their more aggressive neighbors. They show no social advancement over the giant Australian types, and their social life is much the same. They have become secondarily modified, however, in response to the underground life which they must lead. Their size is much reduced, their eyes are vestigial or absent, their mandibles have often assumed peculiar forms and are useful in trapping subterranean

prey, their colors are dull, and their motions slow and furtive. They are *par excellence* the gnomes and dwarfs among ants, the closest imaginable analogues to the forest pygmies of Ituri. In consequence of their inconspicuousness and their willingness to occupy the least desirable part of any environment, they are much more widely distributed over the earth than their bolder but equally unadaptable Australian cousins. But their origin seems to have been to the eastward and to have occurred certainly in a warm interglacial period, and their present distribution shows the effect of this. They are much more numerous in tropical regions throughout the world than in the temperate, and indeed, scarcely exist at all in the western hemisphere north of the Canadian border.

The subterranean members of the Ponerine subfamily differ but little from their more conspicuous congeners in social structure. Some of them, indeed, seem to approach even closer to the ancestral form of organization. Many of them occur in the northern states, and can, with patience, be induced to live in glass nests, where every detail of their social life is continuously visible. It is only upon observations of this sort of these "living fossils," extending over many years, that reliable conclusions may be based.

We may take as our example of a typical Ponerine society an ant that is not uncommon in the northern United States, and upon which continuous personal observations of this sort were made by the writer for many years—the ant *Stigmatomma pallipes*. *Stigmatomma pallipes*, although it occurs generally throughout the United States, is most closely related to a very primitive Australian group, the *Amblyoponæ*. In all probability

it represents an outlying division of that group, which, cut off from its homeland by the change of continents, has yet managed to survive the millenia by virtue of its timid nature and its clandestine habits. *Stigmatomma* lives wholly underground, inhabiting the denser portions of our coniferous forests, and nesting beneath the heaviest rocks, or running its galleries beneath the leafy coating of the forest floor. It can survive only a short time in the open air, and the nearly blind workers never see the light of day, which is known to the queens only upon their short emergence. The colonies are very small, and are composed wholly of one class of daughter workers, as large as the mother queen, and differing from her only in peculiarities of body structure and in their absence of wings. Each ant of the colony is a huntress, for the society is a wholly carnivorous one. Her prey is pursued individually in underground fastnesses, is seized and stung to death, and, if the huntress be famished, she ceases for the time to be a social insect at all, and forthwith settles down to devour the catch. Yet when the edge of hunger is slightly appeased there asserts itself a curious instinct common to all social organisms, and perhaps the most basic one in the organization and maintenance of a society. The huntress is still far from sated, yet, before she finishes the meal, she returns to the colony, painfully dragging her prey with her, to share it—to her own disadvantage—with her mother and her sisters. Exactly so do members of human society of somewhat baser types perform remarkable feats of courage or endurance or sacrifice for no better or less selfish motive than the approval of their fellows. We shall have occasion to return many times to examine

the influence of this "social pressure" in the lives of more advanced ant types.

The relationship of the adults of the *Stigmatomma* colony to the developing young is of the crudest sort. All of the finer nuances of social life conspicuous in the higher ants are wanting. The young larvæ are left to battle for themselves over fragments of insect and other Arthropod prey which have been cut up and indiscriminately spread among them. The young are, for ants, extremely athletic, competent, and able to care for themselves, exactly as the children of primitive peoples display an early competence which belies their later deficiency. Yet the "social consciousness" of the larvæ and of adults is of the rudest sort, and larvæ will attack and devour whatever they can get, including their own brood mates, or even their own nurses, if they can overpower them, as occasionally they do. When mature, the larvæ spin thick and tough cocoons, in which activity they receive some attention from the adult sisters. This attention constitutes more of a hindrance than a help, in fact, and larvæ do much better in this when left alone. When the time for hatching approaches, the wings of the young insect, if it be a male or perfect female, are fully expanded before the cocoon is cut, and the young workers become hardened and capable of protecting themselves before they attempt emergence. They are capable of cutting the cocoons and emerging entirely without help, although, again, attention is usually proffered by adults present at the time—an attention clearly motivated by the ever-present hunger of the carnivorous animal. No larva of any higher ant can spin its cocoon without the aid of its nurses, nor can it hatch without their help. If it be a queen or male of a

higher type, it hatches with its wings unexpanded, and is aided in this expansion by those around it. No larva of any higher ant is fed exclusively upon bits of prey left lying about it. All others receive much predigested food from the mouths of their nurses, and are themselves helpless creatures, incapable of attacking either one another or their attendants.

As the adults deny the giving of predigested food to their young, so do they deny it to one another, and thus there is absent one of the strongest bonds which maintains intact the structure of the higher colonies—the bond of trophallaxis. It is indeed questionable whether the body structure of this lowly, semisocial ant would permit of such procedure, for its crop, or “social stomach,” which enables the higher ants to distribute ingluvial food to their nest mates by regurgitation, is not well developed.

Whereas among the higher ants much attention is paid the queen, the queens of *Stigmatomma* receive no treatment from their daughters which is distinctive from that given other workers. The queen also continues to perform such routine duties as the excavation of the nest and the care of the young after the colony is mature, and also hunts for it—a condition almost completely unknown among the higher civilizations. As the queen retains many of the functions that she had to perform as a solitary organism, in the sphere of colonial activity, so the worker retains many of hers in the reproductive sphere. Thus workers are usually fertile among these primitive ants, and a good share of the young males of the colony doubtless arises from the unfertilized eggs of various workers.

In such a society, as with a primitive hunting human

tribe, the margin of safety and security for each member of it is extremely small. The hunting stage, among ants or men, implies insecurity and the expenditure of much effort for an uncertain and a difficult gain. Nowhere is this more evident than with *Stigmatomma*, whose whole organization is largely a competitive one among solitary individuals bound together by the loosest and most soluble of ties. Workers when isolated, if properly fed, will live perfectly happily for long periods, without evincing the slightest inclination to return to the parent nest. The members of many primitive human tribes, when they are aged and about to die, have a sense of insecurity at home, and seek a solitary retreat far away from those whom they have known. Their feeling is bound subconsciously to the belief that their ravenous, wholly selfish society, always near desperation in its wolflike existence, will tolerate their presence only so long as they are useful members of it. Exactly this same sort of thing has been seen with *Stigmatomma*, where aged workers die far away, in remote branches of labyrinthine galleries, where none will know of them, nor seek, nor ever find them.

Such is the degree to which the tiny, struggling, carnivorous, competitive society of the early ants has been preserved for us today, in all its perfect detail.

All Ponerines are earth-dwelling exclusively, or at most ascend a short distance into the decayed cavities of trees. All are hunting societies, and for the most part they show no interest in other types of prey, nor yet in hunting their prey in concert. However, among the more advanced groups, represented especially by the genera *Lobopelta* and *Leptogenys* and their allies, there are certain forms in which the members of the colony

do hunt together and in file. These colonies are somewhat more populous than is usual in the subfamily, since their efficient hunting methods are productive of more food. They are inclined to be nomadic. From such species we pass through an annectent series of increasingly nomadic forms inhabiting increasingly populous formicaries, until we reach the apogee of development of the ever-hungry societies in the higher Doryline genera of *Dorylus* and *Eciton*, the driver ants of Africa and America.

Eciton and *Dorylus* both present the spectacle of a society which has tried to evade the ancient law that no permanent large consociation of individuals shall be of purely carnivorous habit. The ants are indeed purely carnivorous, and the societies which they have developed are enormous, numbering many thousands of individuals. The payment for this violation of an immutable law has been incessant nomadism, in which the higher Dorylines excel, and to which they are irrevocably committed. No one who has met the scurrying columns of workers of these ants, all completely blind, yet all exquisitely coöperating in their never-ending haste, winding across the rain-soaked floor of a primitive jungle forest of either hemisphere, can forget the sight, nor, unless he study the columns and the colonies from which they emanate more closely, can he escape the conclusion that some external guiding super-force motivates the army. The observer will be still more astonished when he comes upon the temporary bivouacs from which these columns radiate, composed, as they are, entirely of the living bodies of ants, hanging from stub and branch like an immense, quiet swarm of bees, and serving to shelter the foraging workers on their

return and the immense quantity of booty which they constantly bring in. No one who has followed the migrating columns of the ants, when they shift the entire nest, as they do frequently at certain times, can escape a strong feeling of the inevitability of their action; unless, again, he be closely familiar with them. It is one of the most impressive sights in all nature.

Tremendous physical specialization has accompanied this extraordinary social development among the drivers. We cannot know how far the daughter worker has drifted from the original form of the queen, for the perfect female has become extinct among all Dorylines, for reasons unknown. A special caste of worker has been developed secondarily to play the role of queen. So, in this hypertrophied branch of the ant family, extreme social specialization has been accompanied by actual extinction of the caste which originally formed the society, and the caste has been replaced by a derived form. The true workers among the Dorylines have become differentiated into several castes, which are extremely distinct, but do not appear to have particularly distinct functions in the colony. The larvæ have not lost the habit of spinning the cocoon. The incessantly migratory habits of the ants have led to the confinement of breeding to very definite cycles.

The superficial observer, coming upon the raiding columns of *Dorylus* or *Eciton*, thinks of this society at once as a very advanced and specialized one. Such a view, however, is not entirely correct. Physically, the Dorylines have become highly specialized and they have acquired a set of complex instinct-patterns reminiscent of those of the bees, and which make the whole organization vividly suggestive of a single animal, in

which the workers represent the constituent cells of the body, and the queen and the males represent the cells of sperm and ova. But throughout all the activities of the driver ants, spectacular as they are, the barbaric Ponerine substratum upon which they are based is all too evident. The carnivorous habits, the method of transporting young and prey, the failure of the workers to communicate individually with one another, and the ease with which the entire economy of the colony may be overturned by a very slight alteration in the environment, all bespeak primitiveness. The Dorylines represent, in fact, the culmination and the *cul de sac* of a striking mechanistic evolutionary movement whose end product is a highly coöperative organization of rather low-grade individuals, bound by those rigidly instinctive ties characteristic of the exquisitely coöperative colonies of the bees. Such complex instinct-patterns are characteristic of the Arthropods in general, and especially of the insects, and all too often seriously limit their behavior in the face of new obstacles. It is only to the degree that the higher ants have been able to emancipate themselves from these limitations as individuals and as societies that they are remarkable among insects. For it is in the phases of their social evolution where new problems are naively met and plastically solved that ants come closest to men in their approach to living, and these phases of behavior cannot be exhibited by a group such as the drivers, which are at once individually primitive and socially committed to a high degree of complex specialization.

We must turn rather to the subfamilies of the Myrmicines and the Formicines, and, to a lesser extent, to that of the Dolichoderines, to find the main stem from which

have been developed the greater ant societies of today. The Myrmicines, finding their origin, as we have seen, in extremely remote times as a branch of the Ponerines with greatly increased individual plasticity, spread over the entire habitable globe, and are known today everywhere that ants occur. All of them have retained the ancient Ponerine stinging apparatus, but beyond this point they are greatly modified.

There has been no suppression of the original form of the female among the Myrmicines, but she has become modified, as we have already seen, to permit her to found her colonies amid inhospitable regions. The life-span of the queen has greatly increased, the average stature of the worker has diminished, and the workers have become modified into numerous castes. No longer is the diet rigidly restricted to animal food, although this is still taken by preference. Vegetable food of all kinds is sought and greedily accepted, and nectar is highly prized. Concomitant with this has been developed the habit of feeding the young upon predigested food, regurgitated from the considerably modified crop. The young have changed from the long-necked, athletic types of cylindrically tapered organisms to rather squat, thick-set, helpless grubs, completely dependent upon their nurses for sustenance and care. The pupæ are naked, and require much care. The adult members of the colony, too, have come to rely much upon one another for feeding and attention. Means of communication, including the development and perfection of organs of sound production, have made their appearance. The colony has become a closely-knit whole, while its members still retain an individual plasticity and initiative quite unusual among insects, although

by no means as great as that displayed by the Formicines.

Upon this basis have been erected the great agricultural societies of the Myrmicines. These include the grain-harvesting ants of which Solomon wrote, ants of the Old-World genus *Messor*, whose methods of collecting, storing, and utilizing grains and seeds are widely known. Equally famous are the desert harvesting ants of our own southwestern states, ants of the genera *Pogonomyrmex* and *Ischnomyrmex*, whose adaptation to a desert environment is extraordinarily perfect. Most conspicuous among the great agricultural Myrmicine societies is doubtless that of the Attiine ants, the parasol, or cushie ants, the leaf-harvesters of the American tropics, whose entire complex culture certainly was developed after the separation of America and Africa.

The Attiine ants constitute a compact New-World group of Myrmicines, all of which cultivate fungus gardens, upon which they themselves subsist. The species of fungus, the substrata upon which they are fed, and the nature and size of the colony vary with the degree of social advancement of the species. There exists a great variety of Attiine ants, representing all grades of civilization, from small, timid colonies clandestinely cultivating a tiny fungus garden, and nourishing it with bits of decaying wood and other rubbish gathered at random, to the huge and highly specialized true fungus growers. These impressive insects sometimes have nests as large as a cottage, housing a colony consisting of many thousands of individuals. The queens and males are relatively huge. The members of the sterile caste range all the way from soldiers, which are nearly as large as the queen, down to tiny minims, which are not more than a hundredth as large as she.

Each caste performs a definite function within the colony. The species of fungus cultivated by ants of the genus *Atta* is so specialized to domestication that it has become extinct in the wild state, exactly like the staple grasses cultivated by mankind. It belongs to the Basidiomycete, true mushroom group of fungi, yet under cultivation by the ants it never produces mushrooms of its own. The white, thread-like mycelia are cultivated in vaulted chambers as large as a man's head, located deep within the formicary. They form great loose masses, hung from the ceiling, and binding together cut leaves, plucked and placed there for them by the ants. Normally these thread-like hyphæ are uniform in diameter. Under the cultivation of the ants, however, they are induced to develop knobs at their tips, which have been called "kohl-rabi heads," because of their resemblance to that garden vegetable. It is upon the liquid secretion of these bulbs that all the adults of the colony live, and it constitutes their sole food. The larvæ, moreover, are fed with wisps of the vegetable.

The leaves for the fungi are obtained in the course of systematic expeditions, usually undertaken late in the afternoon. Great columns of ants leave the formicaries, and, ascending available trees in a body, proceed to cut and to bring down great sections of leaves, which are transported to the colony. It is an experience never to be forgotten, when, returning tired and hungry through the misty jungle at eventide, one first stumbles across the foraging columns of the parasol ants, their course marked by a line of waving banners, vivid green against the rain-soaked earth, as they return laden homeward. Once within the nest, the leaves are subjected

to a long chewing process, and finally, much macerated, yellowed, and quite unrecognizable, they are inserted into the fungus gardens.

The physical specialization among the workers of the *Attiines* is mirrored in the marked division of labor in these highest of agricultural ants. The queen is constantly attended by a suitable guard, and cared for, and her activities are restricted entirely to egg-laying. She is constantly fed by her daughters, and takes no thought for the brood or for the nest. The largest soldiers and workers habitually forage and cut and bring in the leaves for the fungi. The size of the pieces which they can transport varies to some extent with the size of the porter, but their methods are the same. The smallest workers, however, rarely leave the nest, and never cut leaves, which, indeed, they are physically incapable of doing. Instead, they devote themselves assiduously to a constant weeding of the fungus gardens. This is perhaps the most remarkable specialized agricultural activity of any ant, for, although it is a fact that the substrate which is constantly inserted in the fungus garden is eminently well suited to the growth of many kinds of molds, and although millions of spores must annually be brought into the formicary by the foraging workers, yet an examination of the fungus gardens invariably reveals only a pure culture of the cultivated fungus. The weeders must do their work well!

It can well be imagined that, in such a society as this, the relations between adults, and between the adults and young, are of the most complex and delicate character, although they are somewhat stereotyped in their pattern. The larvæ, perfectly helpless as they are, re-

ceive constant attention and a regularity of feeding, which, thanks to the constancy of the food supply, is probably greater than that of any other insect. The pupæ, which are naked, are carefully and incessantly attended, and are moved from hour to hour about the colony as the exigencies of temperature and moisture demand.

The carefully guarded, pure fungus culture is maintained intact through generations of Attiine city-states through a striking device, which has become automatic in the social economy. The young queens of the fungus growers are, as has been seen, very much larger than their minute first-brood workers—so large, indeed, that even when they employ the conventional methods of colony foundation (isolate themselves without food for several months and rear a dozen young from their own tissues), there is still sufficient surplus energy to permit the cultivation of the fungus garden. So the last remains of the last meal taken by the queen before her marriage flight are retained in a special pocket located behind the mouth parts and held there until a new chamber is excavated and the entrance to the burrow closed. Then they are deposited upon the floor of the new nest, and from the hard little pellet a new garden is carefully created by the queen. The young garden is at first fertilized with the broken eggs of the queen, and not until the fungus is beginning to flourish are eggs allowed to hatch and the first brood reared. Yet so carefully are conditions kept in balance by the queen that when the second generation of young larvæ is half grown, they in turn are fed wisps of hyphæ from the now flourishing fungus farm.

The Attiine ants represent the apogee of the develop-

ment of an agricultural civilization among the Myrmicines and, indeed, among the living things of the earth, if mankind alone be excepted. The Attiine society, however, is but one of the culture-types that the Myrmicines have produced. Pastoral groups, thief ants, temporary social parasites, permanently parasitic forms in which the worker caste has been abandoned, hypogeic forms, epigeic forms, bold conquistadors, all have sprung from this versatile and prolific group. All have been made possible by the fact that individual advancement preceded social growth among the Myrmicines, while the reverse was true among the socially impressive, yet relatively stereotyped, Dorylines.

Magnificent and relatively plastic as has been the development of the Myrmicines, certain features mark them today as far from the most plastically adaptive of ants. The very complexity of the social forms of the higher orders, the relative sluggishness of the individuals of the colony, the widespread reticence to accept change which most Myrmicines exhibit, the sanguine disposition of very many of them, the thickness of their chitinous armor, and many other features, all mark them as somewhat past the apogee of their development. They are a people whose magnificent future lies very largely behind them.

Man has been described as an animal that is congenitally overdeveloped in his reaction to stimuli—an animal, in fine, in which excessive reactions to external conditions have become so ingrained that exciting stimuli are essential to his happiness and continued well-being. Social advancement, as we understand it, indeed, is marked by this hypersensitiveness to the outer world, and by the desire to increase rather than to decrease the



A FUNGUS GROWER

This is one of the northernmost of the genus *Atta*. It collects bits of leaves and the petals and sepals of fallen flowers and uses them to nourish its fungus gardens exactly as its more imposing cousin *Atta sexdens* uses fresh-cut leaves in the New World tropics. This ant is a typical resident of the American South-west. (Saguarita, Arizona. Photo by D. M. Gallagher.)

number of contacts which will produce reactions. The analogue of this state of mind appears to be reserved among ants entirely for the highest members of the sister subfamily of the Myrmicines—the Formicines. Formicine ants may be considered, in anthropomorphic parlance, the most modern type of all, and, in such species as the common red-and-black *Formica sanguinea*, we certainly encounter the pinnacle of Arthropod mental development, although the colonial structures of the Formicine ants are in general less elaborately developed than the best of those of the Myrmicines.

The Formicines, like the Myrmicines, trace their origin directly from the Ponerines, and the more primitive of them are extremely ancient. There seems little doubt that widely distributed, extremely ancient Formicine types coexisted with the Ponerine fauna even in Mesozoic times. The distinctions between the very primitive Myrmicine and Formicine ants are very largely formal ones, and it was not until much later that they became real in a social sense. The loss of a sting, the setting aside of one segment of the abdomen for one waist-node in place of two, and some relatively minor internal and external structural modifications, were all the marks that there were to distinguish the early Myrmicines, Dolichoderines, and Formicines. A much greater and more fundamental distinction and selection occurred during the glacial epochs. For among the warmth-loving Ponerine, Myrmicine, and Formicine ants with which the tropical forests of America and Europe were populated during pre-glacial years, certain hardier forms were developed. These belonged very largely to the Formicines, and, as the ice-sheets pushed down from the north during glacial times, these were rigidly selected from

their less enterprising fellows, which must have perished by countless millions. In North America this wholesale extinction of races must have occurred almost to the southern states. In the Sonoran province, and in the warmer and more arid belts of our southwest, some of the ancient forms managed to survive, but, especially upon the eastern seaboard, nearly all of them must have vanished.

The recession of the ice sheets from this inhospitable land, however, was promptly followed by an invasion of ants into the newly opened territory. Hard upon the edges of the melting glaciers there pushed forward from the south an aggressive, sensitive band of pioneer Formicines, alert to take full advantage of the territory which their less enterprising congeners failed to appropriate. The new land thus became the heritage, as it does in human migration, of the most alert, hardy, and daring types, and they have almost exclusively continued in possession of the land today. And so we find, as the dominant ants in those portions of our globe which were rendered least hospitable by the last ice sheets, a culture of ants characterized by individually highly aggressive, highly plastic forms, which, however, are relatively inconspicuous in their societies. Such are the ants of the genus *Formica*—well known as the "black ants" of the pavements, or the red-and-black ants of the fields. Their colonies, though large and extremely efficient, are by no means so impressive as those of the Attiines. Yet the intellect of the individuals composing them, as measured by standard tests, is far superior. Throughout these cultures, simplicity in all that pertains to social life is evident. The exquisite polymorphism that has been developed to an almost unbelievable ex-

treme among the Myrmicines has been abandoned as too cumbersome by the highest Formicines, and only one most efficient caste has been retained. So the Formicines have returned, in their monotypic workers, to the condition of their primitive Ponerine ancestors, but with the enormous advantage that they have been able to select, in an evolutionary sense, the most efficient from a galaxy of castes, and to discard the rest. How truly has it been said that advance, for man or other creatures, takes the form of a spirally ascending curve!

The heavy, exquisitely chiseled armor of the Myrmicines is completely discarded among the higher Formicines, and there is substituted a very thin chitinous investment, permitting a much greater sensory contact with the outside world. The temperament of the highest Formicines as individuals is totally different from that of the more advanced Myrmicines. In place of the deliberate, sanguine, orderly behavior of the highly invested harvesters or fungus growers, we find nervous, highly reactive and excitable individuals, prone to investigate new situations without delay, and to act upon them with explosive rapidity. The habit of feigning death, a purely structural nervous peculiarity characteristic even of very many of the higher Myrmicines, and noticeable among the lower Formicines, is completely suppressed in the higher members of the latter group, which depend instead upon resourcefulness and swiftness of limb for protection.

The intercolonial relations of the higher Formicines are as different from those of the higher Myrmicines as we may imagine the life of a feudal town to have been from that of a modern city of comparable size. The same exquisite care of the young is to be found,

and the same delicacy of adjustment in the relations between adults. There is the same activity of mutual feeding, the same mutual solicitude for various members of the colony, the same special consideration shown the young queen. But the functions of individuals in the colony is far more flexible than among the specialized Myrmicines, although it is less so than with human societies. A single worker of *Formica sanguinea* may play a great number of roles within the colony during her life. As a very young ant she will remain in the nest and care for the brood exclusively, being fed by her sisters. Somewhat later she will make tentative trips from the nest to forage. At first these will be short, and she may be brought home bodily at the end of the day by some more experienced sister when she herself has become confused and lost her bearings. As she grows in experience, these trips will become more extended and of increasing difficulty. Many ants doubtless become lost on these periodical foraging expeditions, and each young generation is rigidly selected for those individuals with superior ability to return homeward. When her days as a forager are ended, the aging worker, now consistently well fed, may partially usurp the function of the queen, and become the parent of many young males. No such flexibility of function is possible among the lower castes of the higher Myrmicine ants.

The Formicines include among their group representatives of all the cultural stages which ants have attained. The hunting stage is represented among the most primitive of them, which are much like their Ponerine progenitors. The pastoral and the agricultural stages are well represented. Many strikingly unusual cultures are included. Such are the gall-dwellers, with a specially

developed caste whose function is the plugging of the entrance to the oak-gall home, and the silk-building ants of India, of the genus *Ecophylla*, among which the cocoon-spinning larvæ are used as shuttles in the construction of the wholly silken formicaries, and must thereafter themselves pupate without cocoons. The institution of slave-keeping reaches the apogee of its development among the higher Formicines, and Formicine ants have enslaved more species of other insects and lower Arthropods than any other group. The most complex relations of predatory behavior and of parasitism are developed here, both of ants upon one another and of insects originally kept as pets upon their mistresses. The Formicine ants enjoy the widest world distribution, both geographically and in respect to the types of environment which they can exploit, of any group, and their conquests both of territory and of other animals are the most complete and successful. Their susceptibility to training, as individuals, is by far the greatest, and their appreciation and conquest of wholly new situations in their natural environment by far the most rapid. Their nests, and their mores in relation to the care of the young and their own interrelationships, show much the greatest variability and plasticity within a single species. And, with a few striking exceptions among certain Myrmicines, they show the greatest (although still a very slight) tendency to ignore the hostile boundary which the normal ant colony sets up about itself toward every other colony, of the same or another species, and to accept alien adult individuals at special times, or even, under certain circumstances, to undertake colony fusion and the pooling

of resources. This is a very radical step in a creature so completely colonial-minded as an ant, and marks, as we shall later see, the closest social approach of the ants to modern man.

In short, it seems evident that the Formicine subfamily excels all other ants, and indeed all other insects, today in the degree of its plasticity. Within this group are to be found those races whose approach to the problems which inevitably confront any social organism of the earth corresponds more closely to that of man than is the case with any other Arthropod, and whose attitude toward the unknown, while still very rigid and instinctive as compared with that even of the higher solitary vertebrates, yet approaches more nearly the plastically intelligent attitude of mankind than that of any other organism of comparable social development. We shall have occasion to turn many times to this subfamily in the course of the social discussions of later chapters.

Thus we have reviewed, in the briefest possible way, the rise and magnificent development of ant societies and the more general groups of ants which stand demarcated today. In these groups there are included living representatives of every type of society, from the most primitive hunting one, in which the highly precarious life of the solitary hunter is being exchanged for that of a primitive predatory group, to the most highly involved form of specialized agricultural society, with its consequent suppression of the intellectual faculties of the individual, and back again to the point where a somewhat less highly conventionalized social form co-exists with the highest individual mental endowment ever attained by an Arthropod.

These are the ants, as they live about us today. In the following chapters we shall turn to a more intimate consideration of special phases of their behavior, and to a linkage of the social problems of the ants with those of mankind.

Ants and Men as Individuals

WE HAVE SEEN A LITTLE, in the preceding chapters, of the way in which the races and tribes of ants which people our earth have evolved, and of the manner in which they have come to take up the position that they occupy today. The story, to be sure, is but fragmentary at best, for we must depend upon the scattered bits of evidence which Time has left at our disposal, largely in the form of archaic living forms dwelling in the unchanging parts of the world today, as we have seen. No true pre-ant, or missing link between the ants and the wasps, is known to us, to be sure, either living or enshrined in rock. But beyond this "missing link," the series is far more complete than it is for man. The lines of social evolution, in general, have been quite like those of men, as we have seen. It is because of this similarity that the details of the evolution of ant societies are of such interest to us. Ant societies offer many criteria of our own lives which we can never obtain from a study of mankind.

It is appropriate, then, to turn for a moment from

a consideration of the general similarities in the social evolution of ants and men to the likenesses and the dissimilarities which characterize modern ants and men as individuals—the end product of this long race-growth.

Certain similarities between individual ants and men strike us at once. All of them, of course, are in the nature of parallel developments, brought into like channels as the two creatures struggled with the same problems of existence. The consanguinity of ants and men is a very, very ancient one. They have evolved in separate lines since the time when the worms were first developed, many millions of years ago. So the thought is absurd that there is any direct genetic connection between their habit patterns. These patterns are rather analogues—a reaffirming of the existence of a given environmental condition and of the practicability or impracticability of certain ways of dealing with it.

Ants occupy a position among the invertebrates which is very closely analogous to that of man in the vertebrates. Like man, ants are by all odds the most adaptive organisms of their group, and like him, they definitely occupy a position of dominance among them. Like him, the most dangerous enemies of the world for them are others of their own kind. Whether it be on lonely ocean islets or in the thick of dense jungles, next to nearly perpetual snows or in the burning deserts, there will ants be found, their communities always stable, their bodies always specially adapted to the problems which they must meet. No insect other than the ant is able to found and to maintain stable, permanent communities in boreal regions. No social insect other than the ant exhibits the marvelous adaptability to environ-

ment which permits it to live, now in nests of silk woven from its larvæ, now in paper or carton dwellings, as do the wasps, and above all, in an infinite variety of situations and conditions in the bark or twigs or the decayed wood of trees, or in the ground. All other social insects save the termites form rigid, standardly designed nests, like those of the bees and wasps, whose homes are almost invariant from species to species and of the inflexible, instinctive design of the builder. Wasps and bees, to be sure, do show slight outward modification of the form of their covered nests or open combs to fit them to the trees or cliffs or frames of hives from which they are dependent. But within any one species the size of the individual brood cell, its placing, and its shape, are standard features and are maintained at all cost. The builders would in fact be at a loss were they called upon to construct anything different. Furthermore, their adeptness in constructing this particular design is essentially as great when they are freshly emerged as new, inexperienced workers or soldiers or queens, as it will be when they are decrepit and abraded with tattered wings and broken antennæ. They will have learned very little, if anything, of permanent social value to their colonies by the experiences of their own lifetimes.

By contrast, the nests of ants show far greater variability within a single species. There is, to be sure, a general single environment and a general type of nest-form which is favored by each species of ant to a greater or less degree, so that, in general, one can guess very well at a species of ant by looking at its nest. This preference is analogous to the general house styles in vogue among ourselves, so that all houses of a single district may be colonial in character, while another group may

be of a portable construction. But within those wide limits, the form of nest built by different colonies of the same species of ant varies immensely with the conditions and the caprices of that community. The nest is in every case directly adapted to its situation. Advantage is taken of any especially favorable features of the environment, and undesirable features of the terrain are avoided insofar as possible. Even among the most standard types of dwellings built by highly specialized ants, such as those of the harvesters and the fungus growers, there is still immense variability in the number, size, and arrangement of the chambers and galleries, and the general features of the whole formicary.

Some ants, at the other extreme of individual plasticity, are much more variable, even in the general type of their dwelling. Thus our little yellow thief ant of the fields, *Solenopsis molesta*, a remarkably versatile creature, may live an independent life among the grasses, may subsist as a thief ant, or may become a house ant, at the pleasure of the individual colony. In the first case, it excavates an independent nest at the roots of sod or under and about stones in open meadows, following the general nest-plan used by other field Myrmicines, to which subfamily it belongs, but varying upon it endlessly. In the second case, it artfully constructs its dwelling between the walls of the nests of larger ants, and runs tiny, threadlike galleries, which it alone can traverse, into the chambers of its host, whence it may, unknown to them, rob them of their eggs and young larvæ. When it is a house ant, it abandons all pretence of determining the details of its own environment, and boldly constructs its formicary between the walls and in the floor cracks of the human habitation which it has

selected, taking things entirely as it finds them. Such variability of locale would leave any bee or wasp hopelessly confused and helpless.

Ants in general are very fortunate in the selection of their nesting environment. Earth is cheap and abundant, and needs but to be excavated. A social animal can afford to experiment with it, can afford to make from it a roomy domicile, and can afford to have five or six separate nests if desirable, as many ants do. Earth is also an extremely flexible medium in which to work. Continual alterations are easy to make, and enlargements are readily effected for the price of moving a few grains of soil. Think how much more easily and cheaply alterations can be made in an adobe of our southwestern plains country than in a brick city mansion! Think too how much greater the temptation to alteration is in the adobe, and how much more initiative its inhabitants usually display in architecture than do the brick-dwellers!

The wasps and bees are eminently in the position of the owner of the brick house. Wax and paper are both expensive media in which to work. The one requires long hours of inactivity, with accompanying intense body metabolism, while the other necessitates extensive journeys in search of a suitable raw supply and requires its subsequent laborious preparation. The natural consequences of these disadvantages are conservatism in design and an emphasis on the saving of material, and we see exactly this in the standard brood cell of the bee and wasp.

The brood cell of the bee and the wasp is a further encouragement of social or individual rigidity of behavior in adult colony personnel. It effectively conceals

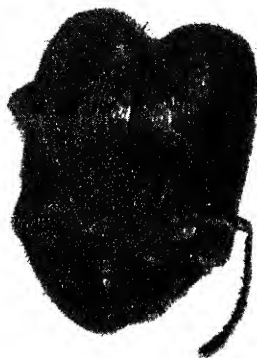


TYPICAL CRATER NESTS

The nest entrances of *Atta texana* in the Arizona desert. (Near Tucson, Arizona.
Photo by D. M. Gallagher.

HEAD-FORMS OF VARIOUS ANTS

Head shapes are conditioned largely by the musculature of the mandibles, their form, and the work they do. Head of harvesting and crushing ant (*Pheidole*, worker) with massive grinding mandibles.



Leaf-cutting ant (*Atta*, worker) with mandibles for clipping thin vegetable tissue.



Head of a driver (*Eciton*, soldier) with jaws overdeveloped and hypertrophied but sharp and treacherous as fish hooks.

(Photos by Gallagher.)

the young larva from its nurses, except for the head, and it anchors it irrevocably in one spot during the period of development. The nurses are thus deprived of an opportunity to become fully acquainted with the anatomical details of their charges during development, and have no responsibility in placing them in the best environment within the nest for their growth. The case is reversed for ants. Lying loose upon the open floor as do the young of ants, the nurses become very fully acquainted with them throughout their development. Furthermore, the adults assume the responsibility of shifting the position of the young from hour to hour of the day, of helping them to build their cocoons when the proper time arrives, and of conducting the even more delicate operation of bringing forth the young perfect insects. Bees and wasps can do none of these things.

Ants, among invertebrates then, like humans among vertebrates, appear as individuals to occupy a pinnacle among their kind, insofar as plasticity of behavior is concerned. Like man, their integrating nerve centers, their true brains, have become highly developed at the expense of their sense organs in general. Think of the imperfections of man's sight when compared to that of the eagle, yet consider the superior integration of the information which he does receive! The huge-eyed dragon fly, or even the rapidly flying wasp or bee, has an endowment of eyes and a development of optic nerves far superior to that of the average ant. But the brain of the ant, like that of man, is much greater in bulk—the integrating center is much better developed. The way of life of an ant is essentially like that of man, rather than like that of the dragon fly or eagle. Both

men and ants are primarily terrestrial organisms, accustomed to a rather reduced range of physical activity, and to the encountering of serious obstacles at every step of their progress. Both are adjusted to an environment in which nothing is particularly easy of attainment, and in which any concerted physical action requires some thought to overcome the resistance to it. How true this is for men is well illustrated by the idyllic dream of floating, which represents the achievement of a great wish for so many of us! Terrestrial life certainly induces myopia and relative physical slowness. Sometimes it leads, as it has among both men and ants, to relative physical incompetence in comparison with winged things. But it also leads to special mental techniques—to much deliberate consideration of obstacles which must be surmounted, to long and serious experiment, to tedious but necessary trial and error—which surely are mentally stimulating.

It is hardly surprising to find that the brains of ants surpass those of other insects in relation to the bulk of the body, as do those of men among the vertebrates. Among ants, however, the evolution has been confined to females. The structure of the brains of nearly all male ants is essentially that of the solitary wasps, with huge optic and antennary ganglia—great tracts for the appreciation of external stimuli—but relatively little tissue devoted to the classification and consideration of it. The queens and workers, on the other hand, show a very marked and striking development of the mass of the brain proper, at the expense of the nerves of sense. This is especially striking in the workers of most ants, since the optic nerves are very far reduced among them, concomitant with a reduction in the size of the eyes

themselves. The brains of worker ants, too, are in general greater relative to the body bulk than among their queens. This, however, is not necessarily an indication of greater integrating power among the workers. It may rather result very simply from the fact that the workers are in general arrested, weakened forms of queens, as we have seen—are in fact, to a degree arrested embryos of queens. It is well known that among many organisms the relative bulk of brain to body tissue decreases as the animal becomes mature, without any corresponding decrease in mental power.

Ants, like ourselves, possess a relatively huge anterior brain, located above the esophagus. But in addition they possess another brain which we lack, the subesophageal ganglion. Originally the purpose of this nerve mass was evidently to actuate the complex mouth-parts. But among the more advanced ants its bulk has greatly increased, and the stems which unite it with the true brain have enlarged and thickened, until in the most modern ants it is so closely united to it as to form a single large mass, pierced by the gullet. It is as if we possessed immense, goiterous masses below our chins, which, however, were filled with nerve tissue, and intimately connected with our brains.

These striking similarities of ants to men are all, as we have mentioned, "convergent" in type, and indicative of how closely two very different creatures may approach one another in their methods of conquering like environmental adversities in the effort to achieve substantially the same ends. We have but to glance at their fundamental individual structural differences and the consequences of these differences to appreciate how striking has been the parallel of their social courses.

The fundamental structural differences between ants and ourselves are essentially those which separate all of the invertebrates from our division of the animal kingdom, and they have placed certain limitations upon the social development of ants that may ultimately become insurmountable barriers to their further progress, and from which we are blessedly free. These differences for the most part concern designs of interior body construction which are basically inferior to our own from the standpoint of the development of that brain power upon which ants depend for their further plastic social progress to as great a degree as do we for ours. Paramount among these differences is that of the circulatory system.

The circulatory system among ants is of an "open" type. A sluggish flow of blood is maintained throughout the entire hollow body cavity, bathing all of the internal organs more or less haphazardly in its oxidizing stream. Motion is maintained in it by means of a tubular heart, which lies dorsally along the inner body wall, with its long axis corresponding to that of the body. Blood, entering one end of this heart, is propelled to the other by a peristaltic movement not unlike that of our own intestines. This blood has far to travel, and its motion at best is slow, while its undirected flow outside of the heart is not conducive to the rapid removal of waste products from the brain or the viscera.

Similarly, the system by which oxygen is brought within the body is inferior in type to our own. A series of branched tubes, called tracheæ, pierce the body wall of the abdomen and the lower thorax. Each trachea is provided at its exit with a valve called a "spiracle." Breathing is accomplished by a periodic accordion-like

motion of the segments of the abdomen, which can easily be seen in the wasps but is nearly imperceptible among ants. At its inner end, each trachea becomes a branched tube with extremely thin walls, and oxygen transfer takes place through these walls to the sluggish blood stream which bathes them. The transfer is not unlike that occurring in our own lungs, but the available surface is much less, and the rate of gas exchange much lower. Ants, in fact, are infinitely more tolerant of suffocation than men could ever be, individuals having recovered after an immersion in water lasting eight hours. By the same token, however, they are normally accustomed to a much lower rate of gas exchange, with all its corresponding metabolic implications.

Ants share with all other invertebrates and with lower vertebrates the disadvantages imposed by cold blood and the practical absence of any temperature regulating system in the body. Their bodies must always remain very close to the temperature of their environment. This condition imposes relatively little disadvantage upon tropical ants. In temperate and arctic regions it limits their activities severely, but, thanks to their extraordinary resistance to long periods at which their body temperatures fall well below freezing, it does not disrupt, but only interrupts, their active colonial life. In this they stand alone among all insects, whose lower members form at best only temporary societies in arctic climes.

The nervous system of ants bears certain unmistakable evidence of its original form among the worms, although it is enormously improved. The typical invertebrate nervous system is that of the so-called "ladder" type. The nervous cord runs along the body, with a node at

each segment, arranged on it like a bead on a string. Each of these nodes gives off branch nerve fibers to actuate the muscles of that segment, and each node acts as a separate coördinating brain functioning relatively independently of its neighbors. We can see this most effectively in a worm or millipede, which, when cut up, nevertheless continues to function fairly normally. Each of the little "brains" manages to carry on relatively independently, but is slightly handicapped by the absence of its neighbors.

Such autonomy of "little brains" is an undoubted advantage from the standpoint of bare survival of the organism, but it is an enormous hazard to the development of mental power. It is essentially an asocial arrangement of nervous tissue, for each tiny center can do no more than barely care for its own work with the muscles allotted to it, and it receives very little help from its companions.

This situation has been very much altered among the ants. The anterior ganglion nodes have been fused to form the brain of which we have spoken, both above and below the gullet. This is an immense advance, for the very much greater power obtained by the massing of all this tissue is of inestimable value for mental development, as it has been in man, who was faced with a somewhat similar situation in his early evolution. Similar fusions on a smaller scale have taken place further down the principal nervous cord of ants. But ants do not approach man in respect to the completeness with which the fusion into ganglionic single masses has occurred. An ant, correspondingly, is much less damaged by having its head cut off than is a man. There is a record of an ant which walked about and behaved fairly normally

for forty days after its head was removed! This was made possible, of course, by the power of the residual "little brains" in the body, which rallied to the rescue and did duty for the "big brain" in its absence, until they were actually starved out of existence. Yet, although this indicates how far behind men the ants are in the degree to which they have consolidated their ganglionic tissue, it also testifies as to how far ants have come in this direction. For no ant ever lived *indefinitely* after the severance of its head, as any worm could do!

All of these features of internal anatomy which we have mentioned tend to limit the heights to which the social development of ants may be carried, relative to that of man. Yet it is not fair to consider this limitation too seriously. Coördinated mental and nervous action, to be sure, is conditioned by the shortness of the tracks over which nerve impulses have to travel in going from one cell to another. In this respect the brain of man has a very considerable advantage over the still-too-scattered ganglia of the ladder-type system of the invertebrate ant. But direct transfer of nerve impulse is but one way of communicating a nervous reaction. Many brains may be effectively massed among highly communal individuals by the simple device of efficient communication, and the advantage gained in this way may do very much to offset a scattered nervous system. An immense "super-organism" can be built up from separate brains, whose only connecting links are the coördinating activities of the animals possessing them. And ants have gone very far indeed, and may go much further, in offsetting the intrinsic physical disadvantage which is theirs in comparison to ourselves by the development of highly perfected social systems incorporating

the individuals essentially as separate ganglionic units. It is precisely because a very perfect social system—which it was within their power to develop—can largely offset the disadvantages of the ladder nervous system, that ants have prospered as they have as communal organisms, and why we may consider their social development superior to our own in proportion as their individual intellect is inferior. The ant community is far closer to representing a single super-organism than any community of humans known to us. It has had both the time and the incentive to develop such a structure; and from this springs its very greatest interest to mankind.

Ants must differ greatly from ourselves in the sensations which they receive from their environment and in the interpretations which they make of them. They approach closest to us, perhaps, in their sense of touch. Even here, however, the differences must be more striking than the resemblances. The sensation of touch with us is rather generally distributed over our soft, sensitive, external surface. Ants, however, are possessed of an extremely hard, insensate armor, which functions as a skeleton, and to which the internal muscles are attached, as they are to our bones. This senseless skin is pierced at intervals by hairs which function as organs of touch, each being connected at its base with a nerve. The sensation, therefore, may reasonably be thought of as rather similar to our own, but it is highly localized—exactly as though our skin were numbed at all except certain very critical points.

The sense of taste among ants gives some evidence of being rather similar in nature to that which we experience. It is, however, entirely separated from smell,



THE DAWN OF ANTS

Workers of *Stigmatomma pallipes*, an extremely archaic form of ant native to the northern states. It is subterranean in habit. The type of the group lives in Australia. Notice the slender, generalized body, with the grasping mandibles adapted to seize living prey and to compensate for its otherwise slow movement and poor co-ordination. It is purely carnivorous, poorly adaptive, and difficult to keep in captivity. (Schenectady, N.Y. Photo by D. M. Gallagher.)

HEAD-FORMS OF VARIOUS ANTS (*Continued*)



Male driver (*Eciton*) with toothless, falcate mandibles.



Advanced Ponerine (*Odontomachus*, worker) with mandibles for seizing distant living prey with a sudden springing snap



Primitive, subterranean, slow-moving ant (*Stigmatomma*, worker) with mandibles for capturing elusive prey in dark chambers and galleries where the ant remains perpetually. (Photos by Gallagher.)

which it is not with us, since we speak of "tasting" very many things which in fact we smell.

The differences between the sight of ants and of men must be profound. Most ants depend for their vision upon their compound eyes—large and relatively conspicuous, two in number, and placed at the sides of the head. These eyes, however, function quite differently from our own. They give an erect image at the retina, instead of the inverted one which is delivered to our brains, and the distinctness of their vision varies with the number of facets which they possess. Since the eyes of most ants possess rather few facets, their vision is probably poor. Furthermore, the compound eye is designed primarily to see moving things. There is much reason to think that, when any insect is at rest, the compound eye quickly becomes quite blind until the insect or an object moves again, since the eye has no lid to refresh it, as do our own, and no power of movement apart from the head. Finally, there is much evidence to indicate that ants are blind to the longer-wavelength portions of the spectrum visible to us—the red and yellow—but are keenly alive to a range of colors to which we ourselves are insensate, in the near ultra-violet. So their color and form world must be a very different one from ours.

There is a greater difference than this, however, from a psychological point of view, between the sense-worlds of individual ants and men, resulting in the relative emphasis which ants place upon the information given them by their various senses. Mankind uses the information furnished by his eyes very predominantly over that given by any other sense. Our dreams are nearly all dreams of vision, only very rarely of hearing, and

almost never of taste or smell. We think of blinding as the greatest sensory misfortune which can occur to us, and are much less afraid of becoming deaf, while deprivation of the senses of smell or taste we consider a mere inconvenience. There is much evidence, however, that ants reserve this predominant sense-position, not for sight, but for their sense of smell, which we have not yet considered. The sense of smell among ants apparently resides in the antennæ, which are essentially everted noses of marvelous delicacy. The organs of smell, consisting of specially modified hairs and orifices with very abundant nerve supplies, are richly distributed over the mobile feelers, especially in the terminal portions, and are intimately intermingled with many organs of touch. The resulting sensation can barely be imagined. It must be a sense of smell whose range and delicacy we, with our extremely poor olfactory equipment, can but dimly imagine, intermingled inextricably with a sense of tactile form, much as the senses of smell and taste are linked for us. This sense has been called the "topochemical" or "contact-odor" one, and the uses which it serves are immensely varied. Information bearing on the recognition of friends and enemies, on its home environment, or on its trails of food sources and noxious enemies, all comes to the ant through this channel. It is a sense which is independent of light, and therefore is of perpetual use within as well as without the nest. The delicately movable antennæ allow the ant to use them as form-gauges. There is every evidence that this remarkable means of contact with the world takes the place in ant psychology occupied by sight in our own, as the sense chiefly to be relied upon. The sense of sight is used extensively only outside the nest, and then only by the

ants which spend much of their time in the open. It may well roughly correspond in importance, under those conditions, with the sense of hearing among ourselves, which becomes important and is to be depended upon in place of vision only under special conditions. The existence of a sense of hearing among ants is problematical.

The world, then, must appear to ants a very different place in which to live from what it does to ourselves. And this difference must be further emphasized by special conditions of metamorphosis and development. Ants, with the rich heritage of complex instinct-patterns that has come to them from their less plastic ancestors, the wasps, owe much of their superiority, as we have seen, to the amazing degree of plasticity which they have managed to superpose upon that framework—in short, to the teachability which they have developed, and the number of individual learning adaptations which the most advanced of them are enabled to make. Yet all, or nearly all, of this learning must take place within an extremely short period of their lives—within the eight or ten days, in fact, which follows their hatching from the cocoon as young adults. For the entire early portion of the life of any ant is spent in inertia, as an egg, a helpless larva, or a more helpless pupa. During the egg and pupal stages, it is entirely out of communication with its colony. During its larval period, to be sure, it is fed and licked by its nurses, receives gifts from them, and in return mechanically donates rewards of exudates. But during this period it is equipped with a very inferior nervous system (the more advanced the adult ant, in general, the more inferior the larva) and it has nothing whatever which can properly be called a brain. Furthermore, when it enters the pupal form, it

effectively exchanges this infant nervous system for one which, although very complex, is not functional. So its hatching at adulthood is very definitely a rebirth into its colony—a rebirth in entirely new guise with a new, impressionless brain as well as a new body. Whatever vague impressions it may have stored up as a larva can be retained only in the most generalized form—far more so than any embryonic or child-memories which may permeate the subconscious psychology of man.

This then is the time-boundary for the brain of a young ant on the side of its immaturity. On the other side, it must look forward shortly to the time when it will have hardened very considerably, mentally as well as physically, when its impressions of the world around it will have become fixed to a very large degree and its days of rapid and “unprejudiced” learning will be largely over. Between lie but a few precious days, and they are used to the best advantage. During these days young ants can be taught to do many unconventional things, such as to recognize traditional enemies as friends, and to associate and even to live with alien species. Under normal conditions this learning is acquired almost entirely within the nest, for once the ant is mature enough to emerge for food, the period of its sharpest mental impressions has passed.

This is a very different story from the long learning time in which young humans may indulge, whose effective immaturity, from a social viewpoint, is so immensely longer relative to their period of maturity than among ants. On the other hand, the instinct-pattern upon which ants have to build, acting as it does as a hereditary informative guide, is infinitely richer among ants than among men, so that many things which the young hu-

man must painfully and deliberately bring within his ken in the earlier days of life are known without instruction to the young ant on her emergence.

The young of the more primitive Ponerine ants emerge from their cocoons almost mature—the young males sometimes completely so. Such ready-made adults have their social learning time seriously curtailed, and, among the males, eliminated. Such a condition would, it would seem, be quite incompatible with the maintenance of a very complex and variable social system. The young of the higher ants emerge from their pupæ in a much more immature condition.

Ants differ from man in another respect which has very interesting social implications. This is in their physical polymorphism, which has already been considered. The origin of polymorphism, and its physiological implications, are but poorly understood today. There seems little doubt, however, that the worker form itself originally, and all the variations which have since occurred from it, represent essentially pathological forms analogous to our dwarfs and giants in human society. But the enormously greater age and sophistication of ant society is nowhere better shown than in the fact that such aberrations have been put to significant social use, whereas man, acting like an essentially solitary but "herding" organism, has all but driven them out and, denying them social recognition, has tried to exterminate them, exactly as flocks of crows or bison drive strange types out of their flocks, or kill them. Ants are extremely tolerant of size differences among their own kind, which man, in general, is not. It is of little consequence to a colony of the fungus growers that the soldiers may be many hundreds of times the size of the

smallest workers. The two fraternize perfectly, and live amicably together. This lack of size distinction, or even, possibly, of size perception, among ants, and its presence in a highly specialized form in mankind, in common with a number of other animals, is probably one of the contributing causes to this divergence of behavior in which the ants have all the social advantage. The other cause doubtless lies in the matter of minorities and majorities. It is clear that a very large proportion of the daughters of the early queens among the pre-ants, which we have already considered, were pathological forms, like the workers of today, and hence were tolerated. Such a system of polymorphism as obtains among many ants might well be built up among ourselves were pathological giants and dwarfs to become extremely common among us. There is little doubt that, in time, we should invent specialized functions which these various individuals would be particularly qualified to perform, and should consider those characteristics which, in their minority, we stigmatize as defects, as of very considerable advantage.

The polymorphism which is so noticeable in the physical sense among ants finds a rather exact social parallel in our own mental polymorphism, which we are only beginning to appreciate. Only gradually and very painfully are we learning that mathematical, engineering, literary, and artistic mutants are born among us every day—in accordance with our general observation that man is an ever-mutating organism, the great majority of whose mutations, however, are mental rather than physical—and it is with even greater slowness that we are sharpening our powers of perception to recognize the mutants and developing means by which their paths

to the specialized portions of society in which they belong can be made easier.

It will be noticed that, whenever we consider ants strictly as individuals, the differences between them and ourselves become very pronounced, and overshadow completely such few individual similarities as may exist. Whenever we consider the ant as a social animal, however, the similarities become especially striking. It is this fact, as has been emphasized earlier, that makes a study of ant societies worth while as a criterion of the background of the guiding forces which have molded the complex basis of our own social structure.

The Rise of the City

THE EVOLUTION of ant society from its inception as a primitive, wasp-like, mother insect with a small, scarcely differentiated brood of young daughters, to the immense and highly complex social structures of modern Myrmicine, Dolichoderine, and Formicine ants has been traced in an earlier chapter. It is an ancient adage of Nature that, among all living things, the principal lines of their evolution shall be retraced from generation to generation by each developing individual itself. We see evidence of such recapitulation everywhere in the growing embryos of animals and plants which, beginning as single primitive cells, gradually develop into colonies not unlike the primitive Hydroids, and then pass through stages closely similar to the final forms of many organisms below them in the evolutionary scale before eventually attaining their majorities, when growth ceases. Such recapitulation is to be seen likewise in social institutions. It is true among the social institutions of man, for who has not marveled at the evolution of the Anglo-Saxon court and the hundred, which he can see

recapitulated in nearly every British colony, or the growth of Latin literature, which France and Spain and all her dependencies have recapitulated so well!

So it is hardly surprising that we find among ants, in the history of the foundation of a single colony, what apparently is a surprisingly accurate critique of the mode of origin of the primitive ant colony. Some modifications have been introduced, to be sure, among modern ants, even in the cases most typical of the present day, and there have been many aberrations. But it is relatively easy to detect the modern falsifications of the ancient document, and reference to the corresponding activity in some very generalized ant will often correct a wrong impression which has been given by a more specialized one. It is of no little interest, therefore, to survey for a moment the various methods of colony foundation in vogue among the ants of today, and to consider to what extent they faithfully reproduce the ancient method and structure of ant society, and to what extent modifications of recent origin have been superposed upon them. We may first of all consider the general fashion in which the great majority of ant cities arise, and thereafter concern ourselves, first, with the little knowledge which we have of colony foundation among very primitive ants, for the additional information which it can give us of the main problem, and thereafter very quickly survey some of the modifications which modern social life has made in the original plan among certain exceptional races of the *Formicidæ*.

The rise of a typical city among the majority of the Formicine, Myrmicine, and Dolichoderine subfamilies follows approximately this course. During the richest

portion of the year, when abundant provender is available and the ant colony is at the height of its activity and productivity, young queens and males are reared in abundance in it. The queens are usually considerably larger than the corresponding worker phases, as we have seen, while the males may be larger or smaller. These sexual forms are usually brought to maturity during the summer in our northern states. Among some species, they remain in the nest from the time of their maturity, which may occur in middle or late summer, until the following spring. More often, however, their release occurs during the season in which they are reared.

Both sexes are winged. While within the parent formicary, they are fed and tended with much care and solicitude by their sister workers. The males, always asocial and essentially colony parasites, contribute nothing immediate to the economy of the city. The young queens, on the other hand, occasionally tend the brood, excavate a little, or otherwise undertake a minor share of the colonial activities. As the time for the mating flight approaches, both sexes become increasingly restive, and may seek, from time to time, to escape from the colony. They are quite commonly forcibly restrained in these attempts by the workers. Eventually, however, the attitude of the workers undergoes a sudden change. Special galleries are excavated to the open air, and even the blindest of subterranean species, whose workers see daylight at no other time of the year, swarm to the surface and out upon the newly made mound, accompanied by most of the young queens and males of the colony. Both workers and winged forms are very sensitive to meteorological conditions during flight-time. More often than not, in our northeastern states, the day chosen will be

hot and humid, with a trace of thunder in the air, and the time of day selected will be mid-afternoon. There is a suggestion of tenseness about the city at this time. The workers swarm about the nest-mound and upon adjacent blades of grass, intensely attentive to the winged forms, which run hastily hither and thither and seek for good vantage points from which to take off on their single flight. If the species is at all abundant, most of the winged members of every similar colony over a square mile or more will be brought out at the same time of the same day. The winged forms, after some hesitation, finally launch themselves into the blue, the active, fast-flying males usually being the first to go. An hour later the air will be filled with the flying forms, while the workers left below slowly return to their own citadels, block the special entrances which they have made, and resume the ordinary business of colonial duties.

The queens, in the meantime, are fertilized in flight, or on the ground immediately below their flight area, a single young queen ordinarily mating with several males successively. Within two hours, as darkness settles and the earth cools, or the threatening thunderstorm breaks, the entire flight is over. The youthful queens descend to bushes, there to rest for a few moments, polish their armor, and await their internal instructions for the next move. The males also come to earth, and seek shelter under stones or other temporary protection for the night. The following day they may come forth again and fly about a bit, but they are entirely unable to fend for themselves in most cases, and within a very few days they perish.

The young, now fertile females, after some hesitation,

descend to the ground, and with much effort dislodge their wings from the wing-sockets. The removal of wings signals the end of an epoch in the life of the female and the beginning of a new one, and, as the diaphanous plumes flutter to the ground, the solitary organism prepares to take up a terrestrial existence which will last for the remainder of her life. She has been reduced essentially to the position of the first of ants, and it is now her duty to recapitulate the whole history of the rise of ant society.

After a short rest the wingless queen begins a feverish search for shelter for the night and thereafter. Rock crevices, chance holes in earth, the undersides of sticks and stones are successively examined until a suitable site is found. The female excavates vigorously here, until a short burrow has been hollowed out and a chamber formed at the end of it. All of this is usually accomplished during the first night. The queen then blocks the entrance to the burrow, and polishes the walls of her chamber to a uniform smoothness within. She is henceforth to be a solitary creature, completely cut off from the world.

A period of rest, sometimes as long as a month, ensues, during which the queen is relatively quiescent, except for an occasional inspection of the chamber walls. During this time, however, important physiological changes are taking place. As soon as the wings are discarded, the powerful and beautifully striated wing musculature begins to degenerate. Phagocytes, invading the muscle-chambers of the thorax, gradually break the muscle down, convert it to fat-body, and pass the fat globules to the now fast-maturing eggs in the ovaries and to the salivary glands. Presently egg-laying is begun. As each

egg is deposited, it is carefully received and tended by the mother, and as soon as three or four are available they are agglutinated into a packet, and given much attention. Young larvæ hatch within a relatively short time, and the course of action thereafter varies with the species. In the tropics, or among those ants which, in the north, undertake their flight in the spring, rearing of the larvæ is begun at once. Saliva, containing the fat-body derived from the degenerating muscles of the thorax, is poured into the mouth of the young larva, and it grows rapidly. The diet, however, is a meagre one, especially since it must supply a relatively large number in this first brood. While still very small and at an incredibly early age, the little larvæ spin cocoons and transform to diminutive pupæ. Among ants of the north, whose queens fly in late summer, winter overtakes the young foundress when her larval brood is only just hatched. Queen and young larvæ then hibernate throughout the winter, their body temperatures often dropping well below freezing, since their burrow is but a very shallow one. The growth of the young is resumed with the coming of warm weather.

One by one the little pupæ come to maturity and are carefully extricated from their wrappings by the ever-solicitous mother. All of them eclose tiny but perfect workers. Thoracic muscles and many of the non-essential organs of the abdomen have been sacrificed for the sake of economy in food-material and time of maturity, but those organs essential to an active, socially productive life—eyes, mandibles, antennæ, legs, nervous system—are fully developed. For a time the new first-brood family remains quietly at home with the mother, hardening its own integument, helping to extricate the

younger sisters, tending the developing larvæ. Within a few days, however, the young workers become restless, and begin to excavate their way to the surface of the soil, breaking through to the light, or to underground foraging territory if the species be a subterranean one, for the first time since the female immured herself, many months before. These tiny, first-brood workers are ardent hunters, and shortly bring in spoils of the chase. The queen-mother then receives food for the first time in many months, and gradually her depleted fat-body is restored. Her thorax, however, remains forever empty, a great cavity taking the place once occupied by the wing muscles—a memento of the sacrifice which made the whole colony a possibility.

Bit by bit the young workers take over the care of the developing brood, and bit by bit the queen relinquishes it to them. The brood, nourished by the outside food supply, increases in bulk rapidly, and the queen, nourished from the same source by this first group of her daughters, lays more eggs. A second generation of young workers matures, somewhat greater in stature than their predecessors, and they, too, soon begin to bring in food. The queen now takes less and less interest in the brood, and shortly ceases entirely to tend it. Much of her initiative slips away, but she lays more and more eggs, and eventually becomes almost entirely an egg-laying machine, relying entirely on her workers to feed her directly by mouth with regurgitated, perhaps partly predigested food.

Thus the city is born. Worker broods appear and mature in ever-increasing numbers, and if the species is a polymorphic one, larger workers and soldiers eventually make their appearance. Finally, after several years at

least, but varying in time with the opulence of the colony, a new group of young queens and males makes its appearance, and the city has attained its maturity. That maturity may be a long one. It will depend, under ordinary circumstances, entirely upon the life-span of the queen, for the city-state is still only an immensely enlarged family, and must ultimately perish with the death of its mother. Eventually, after many years, the sperm stored within the queen upon her mating flight becomes exhausted. Thereafter she will continue to lay, but her eggs will produce the socially useless males, which, after the colony has laboriously spent a season in rearing them, will but fly away, leaving no residue with the colony, and bringing no return to it. This state of affairs may last for some time, during which both queen and workers rapidly become old. The latter, less long-lived by nature than their mother, dwindle in numbers, as generation after generation of males appear and are released. Finally the queen dies, usually quite naturally, within the formicary. Often her body is preserved by her daughters as long as it is recognizable. This treatment is in marked contrast to their treatment of their own sisters, whose bodies are thrown away as soon as life has left them. The remaining personnel of the colony continues its duties as usual. Often one or more workers take over the egg-laying functions of the queen, but since their eggs, too, are infertile, they merely add to the burden of male-rearing. Ultimately, the last workers die of old age, and the city crumbles and disappears, leaving no trace that it has ever been. Yet somewhere else not very far away, a dozen or more young queens live in the midst of flourishing colonies to indicate that

the germ-plasm of the species is far more immortal than any one of its cities.

This process of colony foundation, growth, maturity, and decay, can be considered fairly normal or typical, in the sense that it predominates among Formicine, Myrmicine, and Dolichoderine ants of today. It is essentially the form from which more elaborate and specialized methods are developed, and it probably gives a good general picture of the manner in which the original city was born.

There is much evidence, however, that this picture is not an accurate representation, in all its details, of the founding of the primitive ant community. For this picture, the primitive Ponerines alone can furnish evidence. Very little is known of the methods of colony foundation of the most primitive of Ponerines, and it is here that the most fascinating and significant details might be uncovered. We have, however, one or two hints that the picture for even the normal higher ants may represent a somewhat modified and specialized state of affairs. In the first place, as we have already seen, the queens and the workers of primitive Ponerines are of very nearly the same stature, in marked contrast to the higher ants. It would thus manifestly be impossible for any young queen to isolate herself, to remain for months without food in a closed cell, and to rear from her own tissue a dozen daughters. Two other courses may then be open to the young female. She may return to her own parent colony after her flight, and this may later propagate by division or swarming, as among the bees. Again, she may isolate herself, as do the higher ants, but leave her chamber periodically to hunt and to provision herself and her young, until they are reared to

maturity, thereafter assuming the passive role which she then can afford to take. The solution of the problem is full of interest and experimental difficulties. The second method seems the only one by which ant communities might actually have been initiated. Observations by Wheeler and by the author and others have detected young primitive Ponerine queens engaged in this process. A primitive tropical Ponerine, taken in rotten wood in Trinidad, constructed a very small cell within her larger one, and placed her eggs, when laid, therein. She left her own chamber frequently to forage for herself during the incubation time of the eggs. As soon as they were hatched, the young mother broke the small chamber and distributed the larvæ on the floor of her larger one. Here she brought them food periodically obtained from her own hunting, and distributed it among them, Ponerine fashion. They, as is the custom among Ponerine young, made their own way to the insect fragments and devoured them unaided. Such young workers, of course, will emerge full-size, and thus eliminate the generation of very tiny first-brood workers characteristic of the higher ants.

It is probable that this picture closely represents an accurate recapitulation, carried on today everywhere that the ancient types of Ponerines abound, of the rise of the first of ant communities. The complete dependence upon the wing muscles as a food supply, which enables the higher queen to forego hunting in the interests of giving constant attention to her brood, is apparently a later development. Yet it is already foreshadowed among the primitive ants. Examination of the thoraces of young queens of *Stigmatomma pallipes*, the archaic Amblyopone, and of other ancient Ponerine forms, by

the author and others, shows the same course of degeneration of the wing-musculature as in the higher ants. So this device to aid the young hunting queen in times of adversity is already present among the wasp-ants, and the trend in the higher organisms is toward placing an ever-increasing dependence upon it.

These, then, are the earliest and the normal present-day courses of the rise of the ant cities. Very many modifications have been developed in the procedure, however, which are worth noticing. Most of them have been designed to ease the situation of the queen, to necessitate a less bulky provisioning of her body before she leaves the parent nest, and so, ultimately, to relieve the drain on the parent colony caused by the production of a number of large, young, perfect females. In at least one case, however, the development has been in the reverse direction, and this case we may well consider first.

It will be remembered that the fungus-growing *Atti*ne ants are thoroughly specialized to the cultivation of their own particular fungus, and are quite unaccustomed to feeding upon any other diet. It is therefore of prime importance that a young colony have at hand at all times a regular supply of the precious material. This has led to an extension of the duties and the regimen of the young queen in founding her new colony, which is very striking. We have briefly sketched her behavior in Chapter III. Let us return to examine it a bit more fully.

The genus *Atta* is composed of highly polymorphic ants. The female sex is represented by a long scale of castes, beginning with a relatively huge and bulky queen, passing through a series of soldier and interme-

diate grades, to medium, and finally to very tiny workers, very much smaller than the mother. The mother is an extremely well-endowed organism, physically qualified for the arduous work which she has to perform.

The marriage flights of *Atta* and the isolation of the young queens generally take place in the standard manner for higher ants, already described. One important difference, however, is represented by a small act with immense social implications. Ants in general possess a small pocket, just below the mouth-parts, which forms an island in the long digestive system. In this pocket all the solid material accumulates which the ant takes into its mouth in the course of ordinary foraging. The pocket is lined with powerful muscles, and every bit of available nutritive moisture is squeezed from the solid matter in it and passed on down the gullet. The dry mass of mixed food, residue, dirt, and debris, is then ejected from the mouth of the ant, much as owls reject their pellets of feathers or fur and bones some time after swallowing their bird or mammalian prey. Ants of the genus *Atta* are no exception to this rule, and, since all their food consists of their special fungus, the pockets at all times contain considerable masses of the dried hyphæ of their vegetable. The young *Atta* queen, before emerging for her marriage flight, retains the last filling of this "infrabuccal pocket," with its ingredient of fungus threadlets. It travels with her on the flight, and subsequently. Only after her first chamber is excavated, closed, and finished on its interior, and she has rested for some time, does the young queen eject the packet of debris and fungus upon the floor of the chamber. The fungus begins to grow immediately, and at once the queen shows it every attention, dividing it, rearrang-

ing it, breaking eggs into it to nourish it, feeding it with her own waste products. It grows rapidly, but, although it is nourished by her own degenerating wing-muscles, she does not feed upon it, nor, when her first larvæ are hatched, are they allowed to taste of it. It is reserved entirely for the future, and the queen shoulders the double responsibility of nourishing and rearing both it and her first brood. By the time that her first tiny workers have emerged, the fungus garden is well under way. The first workers, as with other ants, break their way to the surface, but not to hunt directly. Their task is to cut and to bring within the formicary the first leaves, which will go to nourish the fungus garden. Then, and then only, do they cut wisps with which to feed the run-down mother and the developing younger brood.

Among the Attiines, then, there seems to have occurred a development that definitely increases the burden and responsibility of the young queen beyond the median degree attained by the vast majority of ants,—which, again, seems to have represented an increase in the arduousness of the early life of the foundress over the primitive condition. That first increase was accompanied by a widening dissimilarity in the bulk of the female and her first brood, which made the task of the young queen more practicable. The gap in *Atta* is even wider.

This is essentially the only clear case known to us in which the task of the female has become more difficult than the standard one which obtains for most higher ants. There are many extremely interesting cases, however, in which the young queen has, so to speak, successfully evaded her task. The first of these is relatively simple. Among very populous nests of certain higher

ants, especially with certain members of the genus *Formica*, it is customary for the workers, at flying time, to capture young queens of their own species or even their own nests, newly descended from the marriage flight, and to persuade them to enter their old home, to add to its reproductive strength and to lengthen the life of the community. In return for this contribution to an already well-established community the adopted young queen secures immediate food and companionship, and is spared every rigor of the pioneer. Many queens follow this course of action. Sometimes, indeed, the marriage flight is even omitted, the young queen mating within the nest and shedding her wings without ever climbing to the sunlight. Colonies of this habit are characterized by the many fertile queens which they contain and, very often, by their astonishingly long lives as communities.

The queens of many ants among which this practice is a common one show no changes of stature or other structural change, and are quite capable of forming independent communities at will. This, however, is untrue of a large series of extremely interesting forms, among which the slave-making species, to be considered in detail in another chapter, are predominant. Queens of the large red-and-black *Formica sanguinea*, at the time of their marriage flight, are brilliant and look very impressive. Yet it has been found that they are fundamentally incapable of founding their own communities. Often they seek adoption in the populous formicary which they have left, or in an adjoining one of their host species. Such communities, of course, are not limited by the life-span of any of their inhabitants, but may persist as flourishing city-states for periods of many

years. Failing adoption in her own or a neighboring community, the young *sanguinea* queen seeks out an incipient independently founded colony of the slave species, slays the young queen and her first brood of adult workers, adopts the developing larvæ and pupæ, and brings the latter to maturity. The former require feeding, and hence are neglected and usually devoured sooner or later. The stolen slave pupæ, when hatched, mistake the foster mother for their own brood queen, and treat her exactly as they normally would their own, feeding her as lavishly as though she had undergone a prolonged fast.

As soon as the impostor has laid her eggs, the care of the eggs and brood is undertaken by the young aliens. Immediately the young of the adopted species break through to the surface of the soil (or use their own half-formed galleries for the purpose) and bring in provender to replenish the formicary. The young queen, by this device, is required to fast for but a negligible period of time. At their maturity, the true brood of the mother may carry on colonial activities unaided, in which case, as the original group of adopted workers dies away, the colony becomes pure, and is often of impressive dimensions and very long life, giving no hint of its parasitic origin. On the other hand, the workers may inherit the instinct of their mother for the pillaging of the young of alien species, in which case they continue to forage for them throughout the life of the city, to bring them in, and to rear them as auxiliaries in colonial duties. This is the condition among the true slave-makers, which we shall consider in another chapter. This labor-saving procedure of colony foundation, involving "temporary social parasitism," as it has been

called, has been adopted by the queens of a large number of ants belonging to widely differing subfamilies.

In such cases as that of *Formica sanguinea*, which we have just considered, the trick is of fairly recent origin, and apparently has but little affected the stature or outward physical characteristics of the temporarily parasitic young queen. Among the older Myrmicines, and in some of the Formicines, however, the case is quite different. Here very numerous, rather small, aberrant queens may regularly be produced, whose own physical endowment is far insufficient to permit of their setting up their own communities in standard fashion, and whose very lives, therefore, depend upon their temporary parasitic entry into a community of the host species. Sometimes, as with certain ants of the genus *Formica*, such tiny queens may coincide in the parent nest with the normal form, so that, apparently, independent and parasitic colony foundation go on simultaneously. Such a phase, however, seems to be a transient one, for, once the development has started, the larger, independent form of queen is soon discarded.

The reduction in size of the young females which accompanies temporary social parasitism soon leads to a condition of the young queen in which she is herself physically unable to gain forcible entry to the colony which she wishes to take. Conciliation becomes necessary, and this may be undertaken in a variety of ways. Sometimes the entering female, small and timid as she is, contrives to penetrate the formicary unnoticed, and there to live, temporarily, with the host queen. If this condition lasts for some time, the intruder finally manages to ingratiate herself with her hosts, and to persuade them to rear her young. A mixed colony may arise in

this fashion, which persists as long as the old queen lives, but becomes purely that of the parasite queen on her death and that of her workers. The parasitic queen, in such case, usually selects old and populous alien colonies into which she may gain entry, rather than the very young ones, which are chosen by queens of the *Formica sanguinea* type.

In the next stage of this series, the little parasitic foundress, instead of patiently waiting for the host queen of her adopted colony to die of old age or misfortune, attends to the matter herself within a short time after her adoption in the colony. An ant styled with the euphonious name of *Bothriomyrmex decapitans* reveals an especially good example of this type of behavior. Shortly after having gained entry into populous formicaries of the host colony, the queens of this species seek out the brood mothers of the communities, considerably larger than themselves. Mounting the backs of the rightful owners, the *Bothriomyrmex* females spend the next several days of their lives in sawing off, from the top, the heads of these brood queens. As soon as the heads drop, the impostors are adopted by their foster-workers.

The final stage of this development, which is correlated with the loss of the worker caste and the development of completely parasitic habits in the intruder, is represented by a group of species in which the intruding young queen no longer needs to attend to the matter of the assassination of the host female after her entry. This is taken care of for her within a few days by the daughters of the host queen herself, to which they have previously been unflinchingly loyal! We can only surmise what are the forces which bring about such an

activity as this. It is a true pathology of the communal organism. We shall have occasion to survey these developments in other chapters, more especially from the standpoint of the modifications which they bring about in the worker and the queen castes and in the behavior of the parasitic colony as a whole.

Extreme polymorphism may bring about another curious modification in the means of colony formation, representing a mere mechanical adjustment to the standard method. Among some ants of the genus *Carebara*, a South African group that normally lives between the walls of termite mounds and steals and feeds upon their brood, the disparity in size between the queen and her workers may be almost incredible. The huge queens of *Carebara vidua*, which we mentioned in our opening chapter, may be several thousand times the size of the largest of the dwarfish worker caste. Under such conditions, it would be nearly impossible for the young isolated female to rear her first brood unaided, for she would be very likely to crush or to lose them in the process. It has been well established that, in this ant, numbers of the minute workers fasten themselves to the bodies of the young queens before their marriage flight, travel with them during their aerial excursions, and are present, after the first burrow has been dug and finished, to receive and care for the eggs as they appear! In this case, then, despite the great size of the queen, she need not depend upon her unaided efforts to found her colony, though she is by no means parasitic. ✓

Another sort of modification in the normal procedure of city foundation may be brought about by the gradual loss of the true queen caste. This has happened among a number of ants, and all gradations of the development

are known to us, from those in which the true queen caste is becoming uncommon to those in which it is excessively rare, to those, finally, in which it is completely unknown. When such a change occurs in colonial economy, the place of the queen is taken over by a modified worker, whose ovaries distend, and which becomes capable of being fertilized by the males. Such workers, known as ergatogynes, however, never develop wings. They are fertilized on the ground, probably often by their own nest-brothers. This development seems to be a very ancient one. It can be found in progress in some of the rather more modern of the Ponerine ants, where forms are known in which the true queens are rare, but still existent, and in others in which they have never been discovered. The tendency reaches its height, apparently, with the Doryline ants, among which no winged queen has ever been recorded, although the winged males are very well known. So ancient is this condition, moreover, that the ergatogynic worker has become so extensively modified as to be structurally very distinct from the true worker in this strange subfamily!

The effect of the loss of the true queen upon the method of the foundation and rise of the colony must be profound, but we know relatively little of it. Since the modified worker is wingless, and lacks wing musculature, she must be entirely unable to found a colony in the standard way. It is much more probable that, fertilized on the ground or even under it, she returns to her own community, which then splits or swarms, essentially as do the colonies of honey bees in which, of course, the queen has ceased to be independent. Observations on this point, however, are sadly lacking, and are very badly needed.

So, by these devious methods, the city is born. Its original location, and its early fortunes, in the normal case, depend entirely upon the resourcefulness, the natural endowment, and the good fortune of the queen. But, once the first workers have taken over the care of the brood, it is to them that the fate of the colony is entrusted. If the site of the colony is to be changed thereafter, if it is to prosper, and if any of its major policies are to be altered, it is they that must initiate and carry through the development, for the queen, from that point onward, delegates every responsibility save that of egg-laying.

The lives of the first brood of workers are usually short. Poorly endowed in a physical sense, starved throughout most of their pioneer existence, carrying forward in their own little group all of the arduous duties and burdens of colony maintenance, sacrificing themselves very completely for the queen and for their younger sisters, it is not surprising that they wear out soon. Their whole tempo of living has been speeded up in the interest of the saving of the colony. Theirs are active, serious lives, characterized by a very early maturity in the service of an impoverished community. The parallel with human society is very exact. Where, save in impoverished or primitive human communities, do we find very early child-labor and extremely premature adulthood on the part of the youngster, coupled with physical impairment and early death? The human picture differs only insofar as it is affected by the fact that all members of our primitive social groups are equipped as breeding components of it, which leads, of course, to all the phenomena of early child-marriages, which we are accustomed to find among primitive or

poverty-stricken folk. The community can afford no investment in a long, inactive immaturity of its young, during which they are not productive, but spend their time in accumulating physical and mental vigor. Their productiveness must be made available immediately, even at the cost of its ultimate stultification. The generation which is involved unquestioningly pays. It has no choice.

The second generation of the ant city is more fortunate. From the first, it is not obliged to rely for its nourishment entirely upon the salivary secretions of the mother. Its diet is more varied, and the time which can be allowed for its growth to maturity, without immediate colonial disaster, is somewhat greater. Its individuals respond by attaining a larger size before they pupate, and emerge as more robust specimens. If the species is a polymorphic one, the second generation will usually include workers of a somewhat larger caste. If it is monomorphic, the later workers will be definitely more robust and vigorous than their predecessors, and usually of greater life-span.

The subsequent history of the city is principally one of growth. Among polymorphic species, the true soldiers do not appear until much later than the first workers. The increasingly abundant food supply available in the city no doubt influences this to some extent, since, if it is withheld, the soldier caste will not appear. However, an abundant food supply will not guarantee the appearance of soldiers under a given minimum time from the founding of the city. For the young of the soldiers must remain in the immature stage, as a liability to the colony, much longer than the workers, and this does not occur entirely in response to the food supply. A given group of young larvæ, all equally and

copiously fed, will often produce individuals of every worker and soldier caste, the larger individuals remaining as larvæ long after their smaller sisters are fully matured and even, sometimes, being cared for by them. Some germinal factor evidently operates in addition—conditioned, perhaps, by a change in the nuclear chromosome content of the egg-cells of the queen as she herself ages, or, more probably, by changes in the sperm which she carries, as relatively inert cells, throughout her lifetime. It is to these same causes, operating in an ever-increasing degree, that we may most probably attribute the eventual appearance of the young queens in the mature city.

The workers, then, are entrusted with the further guidance of the affairs of the city. They may change its locality many times, carrying their sisters, their queen, their brood, and their pets to the new sites. They may establish summer and winter nests, alternating between them with the seasons, as do some of the subspecies of *Formica sanguinea*. They may establish a dozen or more separate nests, and occupy them all with a single colony. They may, as we have seen, induce young queens to return to their nests at flying time, and so assure to the colony a long life.

The life of the worker or soldier in the colony, though uneventful compared with that of the young queen, is not without its clearly defined epochs. When first hatched, the young worker is, as we have seen, in a soft and helpless condition, and is in the stage in which it learns most rapidly. Bewildering waves of new phenomena flood in upon it, beginning with its own body and the new sense-organs, limbs, and tools which it has so suddenly acquired, and extending to its ever-increasing

contacts with its sisters, their brood, and their environment. The worker makes no effort to forage during this period. Among the higher ants, it remains very quiet for the first day or two of life, and is fed by its elder sisters. Gradually its attention is awakened, first to itself, then to its older sisters, and finally to the brood, which it shortly begins to nurse. During this time, important physiological changes are occurring in the insect, including the hardening and pigmentation of its integument, and, very probably, some perfecting of the nervous system. Among the higher ants in larger colonies, this period of adult youth is a fairly extended one, and the adolescent does not attempt to leave the nest until it is fully prepared. The period of adult adolescence, like that of larval immaturity, is much curtailed among first-brood workers, and is nearly absent among the most primitive Ponerines, where the workers are almost adults when they are hatched, and have their learning period drastically curtailed, but their period of active service to the colony made more immediate.

Once hardened, the average young worker ventures out to forage, above ground if the species is an epigeic one, or in the hard-mined galleries if it is subterranean. The first foraging expeditions are often short and unproductive. The young ant frequently becomes lost. Among the lower species, such strayed individuals usually perish. Among the higher ones, however, they are frequently found, picked up, and carried home by their elder and more experienced sisters. As the worker's fund of experience is increased, the journeys become longer and more productive, and continue throughout most of its life, if it is so fortunate as not to become irrevocably lost in its earlier days.

The course of activity followed by the specialized worker castes may be somewhat different. Among the fungus-growers, for example, the maturing worker, if it is of medium-size or larger, goes forth in a column to cut leaves, but if it is one of the tiny caste (which continues to appear, no matter how old or well-established the city), it never reaches this stage at all, but confines its activities to tending the fungus gardens. The soldiers of many ants take on definitely specialized activities as they mature. Thus those of the harvesters confine their work almost entirely to the crushing of seeds and other hard provender which is brought in, while the gathering of such seeds is left to the workers. Among some of the desert-dwelling ants, certain of the workers, while still in the callow stage, take to soliciting very large quantities of food from their older sisters. This liquid nourishment is passed to the crop, which swells enormously. Ultimately, the young worker so modified becomes quite incapable of movement, and perpetually remains hanging from the roofs of specially prepared chambers, continually receiving nourishment as it is brought in by the active foragers in times of plenty, and dispensing from its ample reservoir by regurgitation when hardship supervenes. This specialized cult, which is joined by one in a hundred or more of the young workers, thus serves as a perpetual food reservoir for the colony.

At full maturity, the average worker of the city becomes somewhat fertile, and may lay rather extensively. The eggs thus produced develop, for the most part, into males, or are eaten at the time of laying by their own mother or her sisters. Occasionally, however, if the queen be killed or removed, one or more workers may

increase their fertility and usurp her function, their own abdomens enlarging to accommodate the swollen ovaries, and produce great numbers of males. It was probably in some such fashion as this that the original ergatogynes were developed.

In death, the worker or soldier often reflects the stability of the community, and the degree to which she has trusted and depended upon her sisters during life. Aged workers of the primitive Ponerines frequently secrete themselves in remote fastnesses of subterranean galleries and there perish alone, as wild solitary animals so often do, where none would expect to find them. It is very wonderful to watch the gradual change of attitude in colonies of such primitive Ponerines as *Stigmatomma pallipes*, both on the part of the worker and of her little primitive community, as death approaches her. The worker first becomes very lethargic, and paralysis of one or more limbs often supervenes. Bit by bit, the remaining workers, and even the queen, come to pay her more and more attention—an attention only thinly veiling its basic hunger-motive. They examine her carefully and in much detail, they lick her with ever-increasing fierceness and attempt to drag her about, though indecisively, treating her exactly as they do their own prey when it is brought in. If she passively remains in the brood chamber, and perishes there, she will be cut up, and the larvæ, ever rapacious, will soon insert their long necks into her intestinal tract and will empty her hard, chitinous shell. Not always will the fierce larvæ wait for death. The author has seen an injured, though yet youthful worker of this species, incautiously asleep while guarding a pile of brood, attacked by one of that very brood, and ultimately killed by the little murderer,

which ate its way into her very vitals. The aging worker in such a rapacious, warlike community usually does not wait for such a fate to overtake her. To avoid being eaten after her social utility is gone, she promptly steals away, and ends her life where her body is rarely found, even as do the caribou of the northern herds.

It is quite different among the higher ants. Here the bodies of workers are rarely devoured except in time of famine. They are merely thrown away when all life has gone from them, and, correspondingly, the worker is able to die in the heart of the community which has reared and nourished her, safe from the last-minute hostility of a fiercely competitive group, and protected from the world outside. There is no existing human community known to us which is so primitive in the treatment of its dead as are the primitive Ponerines. Only among the lower predatory animals, the packs of wolves and wild dogs, and of other loosely federated hunting groups, do we find such conditions. The lowest of men are, in this respect, nearly equivalent to the highest of ants. Thus we see that emphasis once again is laid upon the extreme archaism of social life which the ants permit us to witness among their living forms.

The life of the male ant in the colony is usually short, and precarious throughout. The males of ants are perhaps the most primitive organisms among the stinging Hymenoptera. Their physical endowment is almost exactly the same as that of males of the highly primitive, solitary forms. They have no social instincts whatever. But long contact with their highly specialized sisters has led them to forget even the methods of foraging for themselves, so that they are helpless, for the

most part, away from the parent community. Their existence within the nest, from the time that they hatch until they fly, is generally a passive one. They are treated by the workers exactly like immature larvæ, are fed without begging for food, and are hastily carried out of danger when the colony is disturbed. They wander about the galleries aimlessly, and sleep a very large part of the time. As the time for their emergence from the nest approaches, however, their behavior changes very markedly. They become alert and nervous, and approximate very closely in their behavior an ichneumon or gall fly. This activity culminates in the actual flight, during which they expend tremendous energy, dashing hither and thither in the air, actively seeking their mates. They are by no means impaired by the marriage swarming, and, on descent, can be kept alive for months if they are provided with nourishment. Under natural conditions, however, they are completely helpless on the evening of the mating flight. While the young queens are divesting themselves of their wings, and seeking suitable situations for their incipient formicaries, the males creep into the nearest hollow, or other protection, available. The following day they may become temporarily active, and may even find a little pollen or honey on which to feed. The battle, however, is a losing one from the first, accustomed as they are to the careful attention and oral feeding of their own community. Unable to return to, or even to find, their own city, unfit for a solitary existence, they all perish within a relatively short time.

There are exceptions, of course, to this behavior pattern. The males of the Doryline ants are almost as remarkably aberrant as the wingless queens. They are

large, robust, and competent, and there seems to be some evidence that they return to or remain with their own communities, and even divest themselves of their wings. We know nothing, of course, of the conduct of their mating flight, in which the queens certainly cannot participate; and, except that they are very frequent visitors to lights in the tropics of both the Old and the New Worlds, we know essentially nothing of their subsequent behavior. The males of some of the parasitic ants which we have mentioned are wingless and degenerate. They barely hatch from the pupal state, and immediately mate with their own sisters in the galleries of the nest, after which the sisters fly away in search of alien communities to enter. Ground mating, and brother-sister mating within the chambers of the home community, with consequent elimination of the mating flight, apparently also take place sporadically in a considerable number of distantly related forms.

This, then, is the rise, the growth, and the decay of the city, and of the members which compose it. In its lowest form, it is but a pack of loosely associated, ravenous, carnivorous creatures, exacting immediate social service from all its members, and unwilling to invest more than the bare necessity of time in their development or education. In its highest manifestation it is a huge and independent community, harboring generation after generation of inhabitants which live and die within it, outlasting a generation of men in its duration, investing immense reserves of time and energy in the perfecting and education of its members—a thing apart from and above the pygmy individual lives of any of its inhabitants and even of its queen founder—as truly a super city-state as Athens ever was. In the next chap-

ter we shall attempt to analyze the fundamental ties which cement the units of such a remarkable social structure and around which it has been developed, and to make some comparison with the bonds which unite our own often too-loosely-knit social groupings.

CHAPTER V

The Ties That Bind

WHEN WE COMPARE the motives which bind together the societies of humans and of ants, we are forcibly struck by their similarity. Fundamentally, of course, the purpose of social organization is precisely the same in both creatures—to promote individual welfare and security, to permit the individual to live more peaceably in his immediate environment and to reproduce with greater safety, and to obtain that margin of social security which will provide for his needs in time of famine and uncertainty. Even the attitudes of the individual toward his social group are surprisingly parallel in men and in ants. Individuals of both groups labor under a force which may well be called “social pressure.” We, to a far greater degree than we are usually willing to admit, are motivated in our daily actions and in the whole molding of our life-patterns by our desire that others shall think well of us, that we shall have general approval. This force acts in favor of our societies, since it promotes initiative, individual activity, and healthy ambition. But it is a beneficent

force only as long as the ends of activity which it dictates are in fact those which coincide with the long-term welfare of the society which the individual serves, and which in turn serves him. This is not always the case, either with the individual or on the social plane. Evidence of the former is abundant. We need but to cite the thousands of lives and careers which have been blighted because their owners insisted upon entering a line of professional activity for which they were constitutionally unfit, merely because that particular line of activity chanced to carry social approval and prestige at the moment. Witness, too, the hundreds of other lives which have been blighted because the social estimate of certain types of activity changed suddenly, leaving all the participants in those lines of work who entered it, not for the joy of the work itself, but under social pressure, quite stranded. Evidence is equally striking on the social level. Witness the atrocities that have been carried out by large masses of people in the names of religion and patriotism since very ancient times, when those two great rallying standards for social pressure, of infinite value to society when the ends which they dictate are really of social advantage, chance to be perverted for the time. Social pressure and social approval in any single act or behavior-pattern is far more often a guide for large masses of society than the intrinsic end value of the behavior-pattern itself.

Ants are strikingly similar in their general social attitude. As with ourselves, social pressure is a force for social security so long as its ends coincide with the real good of the society involved, but it may, not infrequently, become perverted. Witness the worker of the higher type of ant, which, famished after hunting, even-

tually captures succulent prey. The first move of the starving individual, if the prey be movable, will be to return with it to the nest, and normally she will take no share of it herself until that return has been accomplished. If the food supply she finds be liquid, she will lap up great quantities of it, store it in her crop, and her very first move on her return home will be to regurgitate it to her hungry nest-mates. Such a move is clearly for the benefit of the colony. It is something else, however, when a nurse ant, in order to feed more growing mouths with the same limited food-supply, abandons her own large queen-larvæ to rear the much smaller ones of a parasitic ant, or even those of parasitic beetles, as may sometimes happen. A normal ant, slaying intruders in the colony, is unquestionably acting in the interest of colony solidarity. Another worker, with equal fervor destroying her own queen in favor of a newly entered parasite of the type which we have already considered, is acting quite differently. Both insects are acting with equal necessity, under equal social pressure, and they have no sense, any more than we have in the great majority of instances, which will permit them to discern the direction in which that pressure is applied. Social pressure, for both men and ants, is a powerful tool, and one that, while normally acting for the good of the individual and its community, is very readily perverted into channels directly destructive to both.

If, then, the social attitudes of individual men and ants toward their societies are strikingly parallel, the actual details of the agents compelling the actions which we see are so fundamentally different as to deserve a chapter, revealing, as they do, the differences in detail

in the way that two ultimately similar societies can be organized.

Human societies, in marked contrast to those of ants, are consociations of small, primitive families, rather than highly developed, single ones. This situation confers advantages on the human group no less than it imposes disadvantages. Since the human state or nation is fundamentally a loose association of an indeterminate number of much more ancient units, it is a very flexible thing, and can quite naturally be expanded or contracted immensely in a short time, simply by adding on or subtracting units. Such additions and subtractions, to be sure, bring their own grave problems. Witness the complications of European affairs after the peace treaties. Among ants, such changes are nearly impossible. The union of autonomous colonies is a very rare thing in nature—their splitting, ordinarily, equally so. Furthermore, the size of most ant communities is strictly limited by the fecundity and life-span of one individual, a fact which is never true of man. The accompanying disadvantages of such a situation for man are quite as great and fundamental. Since the association is both a loose unit and one recently adopted, it cannot be expected that the members will have much instinctive ability in adjusting or resigning themselves to its best good, and this they certainly do not, in very many cases. It is necessary to fall back upon the much older social pressure appeal, under these circumstances, and to impose the force of the approval or disapproval of the society in a measure on all its components, in accordance with the society's intellectual judgment concerning the benefit or harm which their activities may bring it. Such measures, of course, range all the way

from presentation of the Nobel awards to confinement on Alcatraz Island. Coercion of this sort is totally unnecessary among ant societies, and, in fact, would have no meaning whatsoever. The individual in the small ant society is in much the same position as the member of the human family, except that it is endowed with an instinct-pattern sufficient to carry it through whatever specialized duties it needs to perform with far less training than a human would require. The normal human is faithful to his own family, and acts in its best interest even when that may conflict with the newer unit, the state or the nation, which unquestionably, on the average, claims only his second loyalty.

The ant is similarly loyal, but has an additional incentive. The member of the human family is still an independent, unmodified individual, capable of living alone, and moreover, ultimately, of starting a family of his own. He is in the position of the daughters of that first ant-queen, whose remains are not even preserved for us today, so ancient was the time in which she lived, which, winged like herself, ultimately left her to establish communities of their own. The modern ant worker is no longer such an independent unit. She is under physical and physiological compulsion to remain with her own family, for her own best interest. She is rather in the position of the human youngster of five, for whom separation from the family into which he was born constitutes the ultimate in dreaded catastrophes. This condition among worker ants is enormously intensified in the highly polymorphic species. Here the physical, mental, and physiological compulsion extends even to the particular function which she will serve in her family-community. By instinct, by

intellect, and by physique, she is literally and unmistakably born into her job, and, with such highly evolved ants as the fungus-growers, there will be no other at which she can serve. Finally, there is no force whatever preventing any worker that may choose to desert her community from so doing. This actually happens, though doubtless unintentionally, in every new worker generation of any growing colony, as numbers of its members become irrevocably lost on their early hunting expeditions. Thus each group of workers is rigidly selected for those with both the inclination and the ability to devote their entire lives to the society which they serve. The penalty is simple elimination from the community, and from life, purely through the action of forces operating outside the community.

Such conditions make it very plain why an ant community is intrinsically a much more stable thing than any colony of humans can possibly be, and why criminal, or antisocial, action on the part of any member of it, in the sense in which we ordinarily understand the term, cannot occur, despite an utter lack of any intellectual regulatory force, such as a police body. The guiding penalties and rewards are there, but they are supplied, either entirely without the control of the ants at all, or quite automatically, without their intelligent direction. Despite this fact, the guiding penalties and rewards are extremely powerful, and, if we understand them, we will have gone far toward comprehending the fundamental structure of ant society.

The young ant community is at bottom a society that has been formed as a front-line defense against starvation. From the time that the half-starved first brood of the young queen emerges in search of provender

while their famished and exhausted mother awaits within, the family constitutes a hunger group. The workers are small and weak because they have been only half-fed, and they remain but half fed throughout most of their lives; for the greater part of the food they bring in must go to meet the ever-increasing demands of the younger brood. This situation is very little alleviated as the colony grows older. The larvæ, to be sure, are much better nourished, and the adults emerging are therefore more robust, but their days of large meals, easily gained, are ended as soon as they reach adulthood. Thenceforth they, too, share in the responsibility of food-getting, and most of what they bring in will go to feed their mother, or those younger than themselves. It is very probable that in any large and flourishing ant colony, every member except the queen is in a nearly perpetual state of hunger, and this condition, of course, passes all bounds in the case of the driver ants. It is only necessary to offer a bit of food to any member of an ant colony, and to notice its immediate acceptance, to realize how far the whole social structure is motivated by its quest for food, and how far the workers represent undernourished images of young queens, unable to lay or to reproduce at all, primarily because they cannot accumulate sufficient reserves within their own tissues.

It is very natural, under these conditions, that every member of an ant community should constantly be in quest of any evidence of edible material, and keenly alive to such evidence. This quest, in fact, will be the dominating passion of its waking hours. It is well equipped by nature for the search, moreover. We have seen that the beautifully mobile antennæ of ants in all

probability constitute everted "noses" and touch organs of great delicacy of perception. There is much evidence, then, that ants are enthusiastic connoisseurs of odors, forms, and textures, and that certain combinations of these things attract them immensely, while others are equally repulsive. The combinations which exert these specific actions certainly vary greatly with the species, but of their strong specific lure there is no doubt.

We seem to have the key to the principal binding and directing forces of ant society in perpetual hunger, and in the delicately specialized lure of various odors, textures, and tastes. The eggs and larvæ of most ants have strong appeal for adults of their own, and often of other, species, merely as objects to be handled and licked. Thus ants of one species will usually accept the eggs or larvæ of another. The whole sensory approach is very close to that accompanying simple hunger, as shown by the fact that most ants, after accepting and temporarily showing much attention to the eggs and larvæ of another species, will eventually devour them. Ants show much attention to the eggs of their own species, fondling them, licking them, agglutinating them in packets, and rearranging them many times a day. The hunger motive is on the very near horizon even here, for many eggs are eaten, even by their own parents, often as soon as they are laid, and only the surplus above immediate needs or tastes ever hatches. It is presumably the odor or the texture, or a combination of these, which renders the eggs so attractive to their nurses. It is not surprising, therefore, that so many of them should be eaten. The whole situation is very analogous to that of a dog with an especially succulent bone, which licks it avidly for a time before actually

gnawing it, and which may not, for some time, gnaw it at all. In which case, among the ants, the bone hatches into a larva!

The larva is better protected against destruction by its nurses, although that protection is by no means invulnerable, since larvæ are often eaten in normal colonies, especially in times of famine. Larvæ, as soon as they are hatched, exude a quantity of saliva, and apparently also secrete through the skin an oily material apparently containing various esters in suspension. Both the salivary secretions and the exudates of the skin are immensely relished by the ants, which lick them most avidly from the surface of the larvæ, thereby incidentally freeing the larvæ of molds which would be dangerous to them. Now there is much evidence that the quantity of exudate and salivary secretion which the larva produces is roughly proportional to the amount of food which it receives, and, as they grow older, larvæ come to exude these attractive substances principally immediately after feeding. Any young adult nurse soon learns this point, and it is a great help to the larva, both in preserving it from being devoured, and in ensuring prompt and efficient feeding. The average nurse would much prefer to deprive itself of a goodly amount of food, and give this to the larva, in return for the fascinating material which the larva yields in much smaller quantity. Among the higher ants, where the feeding of the larvæ is carried on mainly by regurgitation, the nurses "play the game" with their charges very strictly, and ordinarily feed them whenever they themselves desire the exudates. Among the primitive *Ponerines*, however, where the initiation of many of these colonial ties can be very beautifully seen in its crudest

form, the workers often pinch and maltreat the larvæ for hours at a time without feeding them, with the hope of extracting a little more exudate material thereby.

The link which prompts the rapid and courageous removal of eggs and larvæ from harm's way when an ant colony is disturbed seems fundamentally to be motivated by this concept of the eggs and larvæ as a potential food supply. Among the higher ants, the connection has grown much weaker, and the larvæ receive care and attention far superior to that which would be given an inert supply, but the author has seen workers of *Stigmatomma pallipes* seize particles of insect food which happened to be lying about the chambers of their nest when it was disturbed and hurry them away into dark corners with exactly the same attention as that which was given to the young.

The pupæ of ants, whether enclosed in cocoons or naked, can be attractive only because of their texture or odor, and, among primitive types, they receive far less attention than the larvæ, as they are nutritively less interesting. They are often severely neglected among the primitive Ponerines, and frequently hatch to adults quite unaided. The fragments of pupal skin adhering to the young adult, however, are potentially edible, and accordingly, in a Ponerine colony, the newly emerged ant is soon stripped of any adhering fragments. This stripping is for it a great and salutary service and provides its primarily selfish benefactors with a meal. The entire adjustment between individual and social good in such primitive forms is delicate and beautiful.

Among the higher ants, the development has gone much further. Although the pupæ are not direct sources of food, unless eaten, they are none the less

given great attention, and there is much evidence that they have become attractive in a somewhat derived, "maternal" sense, although the gustatory motive always remains. The desire to extricate the pupal envelope is much intensified; and the pupæ are carefully drawn from their cocoons and the pupal coverings removed. Ordinarily, this process saves the life of the young ant, which would perish without it. It is to be noticed, however, that if the young insect be wounded, or for any reason its nurses proceed to devour its actual tissue in addition to the pupal envelope, this procedure will continue, and the unfortunate will be condemned to execution, cut up, and devoured.

These, then, are primarily the bonds uniting the adults with the brood. In these bonds we have essentially surveyed, although of course in oversimplified form, all the immediate motives that we can discern which bind the primitive Ponerine community together. Primitive Ponerine adults stand in a clearly competitive relation to their young, and this the young are not slow in reciprocating. The competitive attitude of the adults toward one another, moreover, is but very thinly veiled, and shows immediately one of their number is aged or incapacitated, as we have already seen. Otherwise, the attitude of adult to adult among the earliest of ants is one of comparative indifference, much as is betrayed between the members of a loosely federated colony of birds. The adults return with their food to the main colony after their foraging expeditions, primarily to feed the larvæ, and to obtain the larval exudates that result from the feeding and partly because they are accustomed to the colonial environment, and prefer it as a place to rest. Other adults, which happen to be in the

brood-chamber when food is brought in, share the feast, but this is entirely without the intent of the provider. The larvæ, indeed, constitute the most effective binding cement of such a community. If the brood is removed, the colony quickly drifts apart. Through years of intimate acquaintanceship with the details of such family behavior of some very primitive Ponerine ants, the author has come to feel more and more strongly the essentially nutritive basis of their social organization.

Among the higher ants, the indifference of worker for worker has been largely discarded, and the colony is infinitely better integrated in consequence. The movement seems to be the result of two circumstances. The first is that of the somewhat "derived" interest which the higher ants become capable of taking in things originally nutritive in their significance. This has led, as we have seen, first to much greater care of the relatively unproductive cocoons and pupæ, and, secondly, to a real appreciation of the adults for one another. Such appreciation, however, receives tremendous practical reënforcement from the habit of regurgitation, which is totally absent, so far as we know, among the cruder Ponerines. Concurrently with the development of a distensible crop or "social stomach," which can be emptied or filled at will, among the higher ants, has come their habit of filling it to its ultimate capacity when in the vicinity of nourishing liquids on their foraging expeditions, extracting but a very small quantity for their own personal use, and distributing by far the greater portion to their sisters on their return to the formicary. This distribution appears to be a pleasurable act for the giver, and is taken most gratefully by the recipient, which in turn imbibes more than is needed

at the moment, and redistributes the excess to other sisters or to the brood. Thus a quantity of liquid food brought in by one foraging worker is shared among a very large number within a surprisingly short time. A whole system of signals, very readily recognizable for any given species of ant, has been developed about this act, whereby a hungry ant solicits a meal from one returning full-fed.

The habit of regurgitation has contributed immensely to colonial solidarity among all the higher ants. The strong bonds which have united the adult to the larva from earliest times, and do so today even among the primitive social wasps, were thus extended, in equal intensity, to all adults of the community. The whole act, on a somewhat different plane, is reminiscent of our own social pleasure in regurgitating to a community such informational provender as we may have picked up, exemplified by the telling of stories among primitive peoples, gossiping, lecturing, and the writing of books in modern society. In such procedures, pleasure comes to both the donor and the receivers, and the analogy is probably one of the best which we, in our predominantly intellectual society, can conceive.

The social bond which is set up between adult and adult in the higher ant communities is strongly reminiscent of that set up in human relationships by the social attraction of a magnetic personality, but is carried to a far greater extreme. The individual who has a winning personality at first succeeds in a human social group to which he is unknown, regardless of whether he be a useless or a useful member of that society. Similarly, if he is possessed of unattractive superficial characteristics, he finds initial entry into the group and the attainment

of a sympathetic hearing very difficult things, however advantageous it may be for the society to accept him. Much initial effort on his part is required to overcome this handicap with every new group which he enters. Only after a considerable time does it come to evaluate the more fundamental qualities of these newcomers, and ultimately, to be sure, they are judged almost solely in terms of such traits. The case is very similar, but much more extreme, among the ants. Given familiar or pleasing odor-characteristics, the worker of a colony may succeed under all circumstances with its colony sisters, quite regardless of whether it is a benefit to the colony or not. Contrariwise, given the repellent contact-odor of a stranger, the most efficient and energetic of ants will soon be slaughtered in an alien community. In such cases, there is no ultimate recognition of the social value of the individual.

The situation goes very much farther than this, and it is due to its inherent limitations that nearly all the striking and bizarre cases of ant parasitism are enabled to exist. We have already considered briefly the ants which are socially parasitic upon others, and shall have much to say of them in a later chapter. It seems fairly certain that the young parasitic alien queens which so easily gain entrance to healthy colonies and ultimately deprive them of their own fertile females, accomplish this result through the possession of extremely attractive "gustatory personalities," which are never seen through by the individuals which they dupe. *Formica sanguinea* acquires her young colony by sheer force and without guile, but the species of *Bothriomyrmex*, which we have already considered, and all their ilk, are much weaker, individually and collectively, than the communities

which they invade. They become the objects of much undeserved attention, and eventually bring about conditions of social perversion that can only be associated with extreme sensory satisfaction. There seems very little doubt that this satisfaction is gustatory. Some of the little parasitic queens, indeed, are actually provided with tufts of long hairs or "trichomes," which are apparently saturated with attractive ethereal materials highly prized by the host workers, which spend much of their time licking these trichomes and tending the bearers of them.

Ants are by no means the only insects that know how to exploit these rather rigid devices which make for social solidarity among the independent species. More than three thousand species of insects are harbored in ant colonies, for one purpose or another. Some of these, such as the "cows" of which all of us have heard, the aphids, leaf-hoppers, Coccids, and sometimes the larvæ of small butterflies, are kept intentionally, for the sweet secretions which they produce. But a large class is in the formicary purely for its own purposes, and the benefits derived from the association are almost wholly on the side of the parasites. The order of insects having the greatest number of representatives in this situation is that of the beetles, and here we can trace a complete evolutionary series of parasites. It begins at one end with species which are mere marauders of the colony, which lie in wait in dark corners to pull down and devour aged, infirm individuals and the helpless young, and which are persecuted and hated by the ants, and driven out by them whenever possible. These species, which include particularly the short-winged Staphylinids, are analogous to the wolves and jackals lurking

about primitive human settlements. The ants are under no illusions as to their destructive character, but they have much difficulty in detecting or catching them, for these creatures are very alert and move swiftly and stealthily, and the bodies of some of them are so hard that, even if they are caught, they risk little damage and escape very soon, to take up their old occupation.

These beetles clearly possess topochemical characteristics extremely distasteful to the ants. But in a more advanced group of beetle parasites this has very largely changed, and the creatures are regarded with indifference by their hosts. They come to live in the main body of the nest, and slip about without interference, stealing food where they find it, and occasionally devouring the young brood. They are particularly fond of appropriating drops of food in passage from one ant to another during regurgitation, and the cheated hosts, unable to do anything about the matter, can only assume a puzzled and disappointed air.

The most highly specialized of beetle parasites, of which we shall have much to say in another chapter, has adopted exactly the means of ingratiating in the colony assumed by the most perfectly adapted of the parasitic ants, and has carried these devices much further than the Formicid parasites. The beetles of the genera *Lomechusa* and *Atemeles* are large, conspicuous, short-winged creatures, characterized by the presence of long tufts of golden trichomes, which evidently are covered with a film of an attractive substance, since the ants are fascinated with them, and, by extension, with their owners. Lomechusine beetles wander at will about the ant-nests, begging food from time to time from the ants exactly as an ant larva would, and being

fed in the same way, after which its trichomes are licked avidly for secretions, just as the larva is for exudates. The beetle is viciously predatory, however, in more ways than one. Although relatively well fed by the ants at all times, it does not hesitate to devour ant eggs and larvæ in quantity to supplement its diet. Its own eggs it leaves scattered irregularly about the nest. Evincing the same mechanical extension of interest in these eggs (which bring them gustatory satisfaction) that has produced such close coöperation among the adults of the higher Formicids, the ants secure the eggs and lavish upon them the greatest attention. The eggs hatch into fat, white grubs, not too unlike ant larvæ in their general conformation, and these are promptly adopted by the foster-parents, fed, and given care greatly exceeding that lavished upon their own young. The beetle larvæ grow rapidly, lying relatively quiet among the ant-young. They, like their elders, devour the ant larvæ among which they are placed from time to time, and attain a healthy maturity in short order.

Only one error in the conduct of the life of *Lomechusa* prevents it from immediately overrunning and destroying the host colony of ants whose social instincts it has so completely exploited. The larvæ of the beetle normally pupate underground, and the pupæ must remain covered with earth until ready to hatch. The necessity of being buried is well understood by those ants whose own larvæ are accustomed to spin cocoons, for these are habitually buried while spinning, in order that they may have material to which the delicate silken threads can be attached. However, when spinning is completed, the ant larvæ are disinterred and carefully cleaned, and herein the requirements of the ant and the

beetle larvæ radically differ. True to their traditional methods of larva-culture, the adult ants carefully cover the mature larvæ of *Lomechusa* and permit them to transform to pupæ. Thereafter, however, they dig up and clean all the beetle pupæ which they can find, just as they would their own young. The beetle pupæ promptly perish under this treatment, and are thrown away. Were the ants quantitatively accurate at finding all of the larvæ which they have buried, they might soon rid themselves of their parasite. Unfortunately, however, they are not, and a new *Lomechusa* population springs from the forgotten young.

Beetles of the genus *Atemeles* have carried this association still further, to the increased disadvantage of their socially blind hosts. They are more agile as adults than *Lomechusa*, pay considerably more attention to the adult ants in the colony, and have actually learned the signals ordinarily used by adult ants in soliciting regurgitated food from one another. So, while *Lomechusa* is fed and treated like a larva by the ants throughout its own larval and adult life, and is perpetually regarded as a somewhat helpless, passive, and immature creature, socially speaking, the adult *Atemeles* is treated by the ants as one of themselves. It is permitted still further freedom in wandering about the colony, in devouring the young, and in robbing incoming adults of all their hard-won provender, which the ants are only too willing to surrender.

A colony infested with many of these parasitic beetles may go to amazing extremes in its insane hospitality toward them. The beetles and their young are fed and tended at all costs, however much the ant young themselves may suffer from neglect. Heavy parasitism by

Lomechusa and *Atemeles* ultimately results in the production among the younger generation of adult ants of a highly pathological, perverted form known as the pseudogyne. It appears to result from the last-minute modification of a neglected queen-larva toward a smaller worker, although this derivation is not positive. In any case, it is certainly intermediate between the two castes. It usually possesses three simple eyes, in addition to its two compound ones, like the queen, and its head in general is of the shape of the queen's. Its thorax contains provisions for wing muscles, but there are no wings. Its stature is that of a worker, and it is usually poorly pigmented, and lighter in color. These individuals have very little energy, and are lazy and ineffective in both the work and the defense of the colony.

As colonies become more and more heavily infested with their insidious beetle parasites, these pathological individuals appear in greater and greater abundance, and ultimately they weight the whole social structure so heavily that it breaks down and the colony perishes. Strong communities of such ants as *Formica sanguinea*, which normally would live for many years, can be reduced to pitifully small remnants in a surprisingly short time when occupied by *Lomechusine* beetles. We shall have occasion to examine these ant parasites in another chapter, and to consider the relationships which they bear to certain social racketeers in our own societies. Here we may be content simply to note the example that they give us of the relatively unseeing, unmodifiable rigidity of the ties that so firmly bind together the members of an ant colony. These ties, under all ordinary circumstances, serve perfectly to unite the community; but the ants are helpless in the face of the

proper sort of gustatory exploitation. That the "personality" ties which link us adult-to-adult in our modern societies are not exploited so completely in a similar way is only because of our greater mental plasticity, because we can "see through" our mistakes to a greater degree. The human ties, to be sure, are exploited in the same way, but to a lesser degree, although the error is more quickly rectified. See how far, for example, the charlatan of pleasing personality can go in fooling his public, to their own delectation and disadvantage, and how far the "bluffer" can travel on his bluff in the older sorts of business enterprise. The perception that enables the modern business executive to avoid the employment and support of such unprofitable people has been very hard-won. It is, moreover, far from perfect today, varies immensely with the employer, and is usually achieved only by the combined judgment of many associates. Ants are in the position of being obliged to make "snap" judgments among their associates, and to abide by them, for they have no criteria of subsequent behavior which they can apply within one generation. Were we confined by such limitations, our errors would surely be almost as grave and as frequent as theirs.

The result of the closely-tied association which ants have won for themselves in normal, advanced colonies, rigid though the methods may be, is a margin of "social security" against a hostile environment that shows itself in many ways. A host of harmless insects comes to dwell within the formicary, taking advantage of that margin while doing little damage. The very parasites which we have considered could not subsist as they do were there not a large surplus of wealth to support them. That ants instinctively appreciate this security which



A DESERT WANDERER

Ischnomyrmex cockerelli is a large and handsome desert ant, of great power in spite of its slender build. Its typical home is in the American deserts, where it builds great mounds, sometimes three feet across, which it paves with small pebbles and gravel brought up for the purpose. Workers are frequently to be seen at eventide bringing home stray sisters. It is partly granivorous, but less completely so than *Pogonomyrmex*, feeding often on termites. Notice the ant guest in the picture, an insect closely related to our domestic "silver fish." (Near Nogales, Arizona. Photo by D. M. Gallagher.)

they have won is to be seen in the attitudes of workers of the same species in large and in incipient colonies, and when at home and abroad. An ant of an aggressive species, surrounded by her own sisters in a large colony, will risk her life in attacks and assaults which she will studiously avoid, or from which she will openly retreat, if she is alone or if her colony be young and weak. Similarly, if her colony be strong, she will not hesitate to attack and dispatch a stranger from an alien group, even if of her own species. If alone and in unfavorable circumstances, she will be much more tolerant of the same stranger, and will be inclined to temporize. In this way, two stranger ants which have lost their ways and have accidentally met far from home will frequently fraternize temporarily, their social instincts triumphing momentarily over their habit of rigidly maintaining colonial exclusiveness and solidarity.

Ants, to a degree far greater than that of men, are specialized communal animals. The worker, as we have seen, has been nutritively reduced to the position of a dependent animal, and her actions correspond very exactly to this status. She is, however, not in the position of the specialized worker honeybee, for she can exist alone for long periods if need arise. The bee is incapable of doing this. Once again we see in the ant a greater degree of plasticity than that which we can discover in the bee, although the ant is much less plastic than man.

We have drawn such close attention in this chapter to the analogies between the details by which the social structures of men and ants are constituted that there is a real danger of assuming for the ant a consciousness and a thought-pattern similar to our own. Nothing, of course, would be more erroneous; for we have not the

slightest justification for any such assumption. It is hard not to assume for the ant some sort of dynamic mental process, but we have only to think of the fundamental structural, nervous, and sensory differences between the ants and ourselves to realize how incapable we must be of accurately picturing to ourselves any of the particulars of their inner lives. This fact, however, in no way destroys either the reality or the impressiveness of the many social parallels which we can draw between the lives and organizations of two creatures whose fundamental purposes in living are so nearly the same. Once again, we need see and emphasize only the striking parallel in the courses of two rivers, sprung from widely different sources, but flowing to a common sea!

The Ant Colony as a Multicellular Organism

MUCH EMPHASIS has been laid, in the preceding chapter, upon the solidarity of the ant colony as a whole, and upon the means by which its component individuals are bound to one another. So great is this solidarity, in fact, that the colony seems almost like a plant or animal, of which the ants composing it are but the individual cells. There is doubtless more than fancy in this analogy, for throughout nature single patterns can be found which are of surprisingly general application to living creatures. The growth of the ant colony repeats the struggle in which the primitive single-celled creatures of the world gradually came to cling together to form small, uncertainly bound groups of attached descendants, which, further differentiating, and having an ever-perfecting division of labor, have come to form the exquisitely coördinated multicellular plants and animals of our modern world. The further one pushes the anal-

ogy of the ant colony to the multicellular plant or animal, the more strikingly is correspondence found in the details of their behavior. It will be worth while to glance for a moment at some of the minutiae of this comparison.

There is much in the modern ant colony to suggest a somewhat complex lower animal, such as a chambered nautilus. The males and the queens of ant colonies may be likened to the sperm and the egg-cells, respectively, of the nautilus, which, when fertilized, will become true eggs. Like the sperm cells of lower and higher animals alike, the males are relatively simple and unspecialized, and are very much alike in ants whose queens and workers differ widely in bodily form. Like sperm again, the male is highly mobile, can travel actively, widely, and for long distances, but he has no food reserves upon which to depend, he is very short-lived, and exists but to fertilize the queen. The queen, like an egg, is relatively bulky and well-supplied with nourishment analogous to yolk, and is capable of existing without further food until her first offspring (body cells in our analogy) are mature.

The fertilized and isolated egg of the ant-organism, the queen, begins, as we have seen, with the rearing of tiny first-brood workers, representing the first young somatic cells of the developing super-creature. Like true early body cells, these workers are highly modified, and their entire effort is given in the service of the growing organism. They and the first subsequent worker generations are relatively uniform, and correspond to the first cells of the developing animal body. Like specialized body cells, too, these workers have lost the power to multiply, just as, with a few exceptions, the cytoplasm

of any cell cannot increase its bulk, and, like cytoplasm too, the worker cannot even maintain itself apart from its germinal nucleus, the queen.

As the colony-organism grows, the workers come to be especially concerned with its feeding, defense, and maintenance—in other words, with the management of its nutritive and other internal affairs. They are like the so-called endodermal cells of the body, those through which digestion, respiration, and the other internal functions are cared for in ourselves. Later, as the colony grows older, members of the soldier caste appear. When their functions primarily concern the defense of the nest, they may be likened to the cells of the ectoderm in our multicellular organism—the skin, horns, spines, hoofs, and teeth, which are primarily concerned with the foreign relations of the creature which they protect, and whose principal business is with the outside world, with the conquering of unfavorable bits of the environment.

The community reaches maturity at a rather definite age, characteristic of the species. Like a higher animal or plant, it cannot reproduce itself until that minimum age has been reached. Then the sperm and egg cells are produced, represented by the young males and queens. The colony may be one-sexed, producing only queens or males, or the germs of both sexes may be present, again as in higher plants and certain multicellular animals. Once the colony has attained maturity, it may or may not continue to grow in size, depending upon its species. This, too, is like true organisms, some of which stop growing at the reproductive age, and others of which, like many trees, continue to increase in size from year to year until death. The factors which delay maturity

among ant colonies are almost precisely the same as those which restrict plants and animals in this respect. Poor nourishment, cold, and lack of room in which to develop hinder the attaining of ant colony majorities as much as of those of trees or fishes or men. As among many-celled organisms the sperm and egg cells are cherished in special glands and carefully nourished by the parent organism until they are thrown off, so, as we have seen, the males and queens receive careful attention and protection until the time of their marriage flight, and, up to that time, are in the completest sense dependent upon their colony.

Like animals and plants, colonies of any one species of ant grow to a fairly uniform maximum size under the best conditions, and no change of the environment will cause the colonies to exceed this maximum. An *Atta* colony, given optimum conditions, will attain to immense dimensions, like a forest sequoia, but no force is sufficient to make a community of *Stigmatomma* exceed a population of one or two hundred, just as the little *Oxalis* that grows beneath the sequoia root cannot be forced to attain the stature of the tree that towers above it.

We have compared our ant colony, among other things, to a chambered nautilus. Like the nautilus it has a shell, the nest, which it grows and develops, but to which it is not necessarily permanently attached. Like the removable shell of the nautilus, the nest form may show much adaptation to the conditions surrounding it, especially to the direction and quantity of sunlight which it receives. Like the shell of the nautilus, again, the nest-form is in general characteristic of the species

building it, and like the nautilus shell, it is rarely abandoned, but may be if conditions warrant.

This, then, is the condition of the normal ant-organism—begun among the Ponerines as a primitive group of practically undifferentiated cells, struggling, like the colonies of cells of some of the lowest algæ, to remain in contact with, and to perform crude service to, the whole, and ending with a differentiated organism reminiscent of many of the more advanced plants and animals.

The analogy becomes even more striking when we include some of the socially aberrant types of ants which have already been mentioned. Temporary social parasitism among ants, in this view, corresponds to the method of life of the "strangler fig" of our American tropics. Small seeds of the fig settle in the crotches of independent forest trees. The young seedling, germinating, spreads its roots over the bark of its host, and gradually but surely sucks away its life, as the aerial roots reach ever for the soft black earth far below. Eventually the roots reach the ground, and, as they enter it, the host dies away and the parasite, now on a fully self-sustaining basis, establishes itself in the earth and henceforth grows as an independent tree. Even so do temporarily parasitic young queens enter alien colonies, assassinate their queens, and compel the workers to provide for them, while they slowly establish their basis for future life among their own young workers. Then, when a full force of young daughters is ready for action, the old, exploited, native workers die away, and leave a pure, self-sustaining colony of the invading species to carry on for years to come, with no hint as to its parasitic origin. Such modes of parasitism are risky, both for

plants and for the ant-organism. Plants following this habit, therefore, produce many very small seeds—many, since there is slight chance of survival, small, since those which survive have little need of a store of nourishment, because they can immediately feed upon the host. The ant-organism follows the same pattern. Temporarily socially parasitic ant colonies produce numerous, tiny queens, as we have seen, corresponding to the little seeds of parasitic plants. The analogy is somewhat different in the case of the slave-making ants, in which members of both the slave-keeping and the slave species coincide in the nest throughout colony life. This is more like the permanent composite associations of plant cells of different types, or of plant and animal cells, which we see all about us, and usually think of as one organism. Such are the lichens of the tree trunks, associations between a fungus and green algal cells, and such are the green, many-armed hydras of our ponds, wherein algal cells have taken up their dwelling throughout the tissues of the primitive animal host.

The little parasitic queen, destroying the queen of her host colony, or persuading the worker personnel to do so, can be looked on, again, as a germ of malaria, or as some other nucleus-destroying creature. Entering the complex cell of plant or animal, the parasitic organism destroys its reproductive nucleus, thereby chaining the cytoplasm forever to its power, even as the parasitic queen chains the workers of the colony which she invades.

Last of all, we may liken the development of the pseudogynes and other pathological worker forms which we have already mentioned to the growth of cancerous tissue in animal organisms and to the development of

galls and other deformities in plants. The causes of all these developments are far too little understood today, and future research faces a very great responsibility in elucidating all of them.

Parallels of this sort can be carried very much further, but we shall leave the subject at this point without laboring the issue, since we are primarily interested in parallels between the societies of ants and men. But such comparisons as these are worth brief consideration for a moment to emphasize how far, in fact, ant society has come toward the realization of a highly perfected, if mechanical, social system, and what a thoroughly solidified and organized unit a colony of the higher ants really is. Compared to it, on the social plane, human society is a very loosely and crudely organized colony of dissenting units.

Heretofore we have been primarily concerned with the background of some of the principal features of ant society in general, and have satisfied ourselves with very brief glances at the parallels to be found in some of them to features of the life of mankind. We shall turn, in the succeeding chapters, to a more detailed survey of certain special features in the social structures of ants, and to a more careful consideration of the light that they may throw upon corresponding human institutions.

Fascism or Communism?

HOWEVER PERTINENT or impertinent it may be in these days of institutional crises, we can scarcely avoid asking ourselves how far the exquisitely correlated colonial life of ants partakes of the character of a democratic or a totalitarian state. The query is not an insignificant one. For among ants we witness without a doubt the dominant form of invertebrate life of the world, the most successful experiment in Arthropod evolution which Nature can show us in the world of today. The social forms which, if they are not the cause of that impressive success, have at least been intimately correlated with it, cannot be without interest to us, who are so vitally concerned with maintaining our present dominance among the vertebrates of the world.

It seems a very far-fetched procedure to attempt to distinguish totalitarian from democratic social structures among ants, and a still more difficult and dangerous task to speak of fascism or communism in its meaning of the present day, within the totalitarian division. Yet a somewhat closer scrutiny can reveal the most surprising

superficial similarities in the general social trends of ants and men. The significance of the analogies lies in formal superficialities, as we have seen that it does elsewhere in the complicated lives of these remarkable insects. Close study will show that the means by which similar effects are achieved, are, in their mechanisms, entirely different. In the same way we marvel at the similarity, in form and function, of the race of Australian marsupials (with its fierce predatory Tasmanian wolf, its inoffensive, vegetarian Koala bear, and its browsing, active, kangaroo) to the corresponding groups, vegetarian and carnivorous, among the placental mammals. The significance of the comparison lies not in the fact that the mechanics of the predatory and browsing structures, and of the production and the nursing of young, are radically different in the two groups, but rather in the fact that forms of life which began so differently have finally been led into a common series of molds. Because of this the molds themselves are delineated more closely. And so it is in our comparison of the societies of ants and men. The forces that bind the two societies, which direct their activities, and that promote their welfare or lead to their downfall, are in their details wholly different, as we have seen. But the mold by which large-scale social life has been and will be formed stands out with phosphorescent intensity when we restrict our attention to its outlines.

On this basis, let us notice for a moment the remarkable superficial similarities of the primitive ant colony and the young democracy of the human present and near past. There is much to link the primitive German folk-community, the Anglo-Saxon hundred, the New England township, and the Japanese village-state with a colony of the lower Myrmicine ants, and there is much

similarity between an Iroquoian tribe and a community of primitive Ponerines. The societies of the Iroquois and of the Ponerine "bulldog" ants of Australia are both hunting ones, composed of relatively few individuals, whose status within the community, as adults, is approximately equal. The grown hunting worker of the "bulldogs" and the warrior of the Iroquoian tribe have much in common. Each hunts individually or in very small groups. Each, as soon as the kill is made, returns to the home community with the booty, which is haphazardly shared among the members of the colony. The distribution may be far from haphazard among some human tribes, and may be governed by the strictest and most involved of taboos, but this feature belongs to the mechanism rather than the model of the picture. The success of the personal exploits of each active community member resolves itself into a function of keenness of sense, alertness, strength, agility, and skill in the overcoming of prey. The survival value of the individual to the community depends almost entirely upon his possession of these characteristics, and varies widely with the degree of his endowment. Consequently we find great physical strength, much alertness, and high activity to be characteristic of the members of both groups, and, associated with these, are relatively low powers of cooperation. Each individual is essentially self-reliant, isolated, and self-helping. The share in colonial welfare at this stage of development is approximately equal among all the active individuals composing the community. There is little differentiation into social castes in either society. Essentially we deal, in both cases, with a hunting, tribal democracy in its simplest form.

When we examine the early village-state or the typi-

cally Germanic community as it was represented particularly in early Saxony and in England and Iceland abroad and in colonial New England at home, the analogy to the smaller, less conspicuous type of Myrmicine community of today becomes more striking. The society has ceased to be a purely hunting one, and has become essentially sedentary in the cases of both ants and men that subsist to a large degree upon vegetable food, which may or may not be deliberately harvested in both cases. Personal agility and resourcefulness is much less at a premium in such an organization, but constant, steady coöperation between individuals has become far more important. Humans and ants alike become modified to this condition. The modification is best seen among humans in the America of a hundred years ago, where the resourceful pioneer gave way to the homesteader, who followed him. The homesteader opened and developed the land which the pioneer had won. The former was a believer in simple coöperation. He exploited the land in ways which would never have occurred to the pioneer, but detested the constant restlessness and the complete reliance upon self which were the watchwords of the earlier comer. The communities of more primitive Myrmicines, like those of the California pioneers in 1849, are still "open structures," in which the activity of each individual is of great importance to the welfare of the colony. All capable members of the community, moreover, are of essentially the same value to that community, if we except the queens and males in the ants—forms which we shall consider later. Consequently, among the societies of both the democratic men and of these ants, we still find a nearly equivalent endowment for all individuals. Such equal-

ity results in a certain stereotyping among men, which one can notice even today among such of these small communities as still exist, and monomorphism among the workers of the ants. Genetic as well as selectional factors no doubt operate here also, but with the mechanism we are not now concerned.

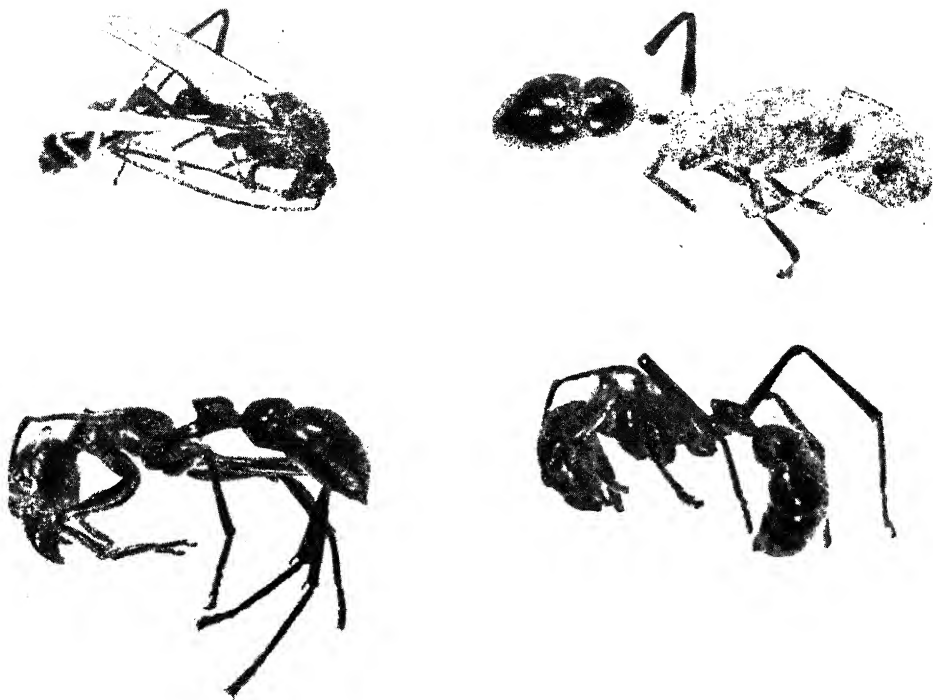
Ant societies of this type are today essentially "non-expansionist." We have seen that the Ponerines, as a group, are now a retiring society. They have been forced out of the most desirable situations by more social and better-organized types throughout the temperate world, and are fast giving ground even in their native tropical rain-forests wherever more compact groups are invading their seclusion. The small, sparsely colonial forest Myrmicines of the present day are of somewhat similar stripe, although they are more able to maintain themselves in the face of adversity than their exclusively meat-eating precursors. But all of these communities are peace-loving, with no more than very minor designs regarding the conquest of territory or food sources. To avoid any sort of conflict with their enemies, they are willing to deprive themselves rather severely of both food and land, or to adopt extraordinary and inconvenient means of exploiting territories either unwanted or overlooked by their more powerful adversaries. It is far otherwise with certain types of ants, as we shall see in another chapter. In this respect, also, the societies of Ponerines and early Myrmicines markedly resemble the more conservative sorts of human democracy of all ages, wherein the emphasis of the individual and of the community is on the improvement and consolidation of the relationships of those composing the group, rather than on any sort of world conquest.

These are the truly democratic village-states of the ants of today. An early offshoot of the hunting community, as we have seen, were the Dorylines, with their large increases in numbers of the hunting community, and a development of a degree of excitability, restlessness, and conquistador aims wholly at variance with the stock from which they came. In the societies of ants and men alike this phase of communal development must of necessity be a highly transitory one. The state of intellectual and of fundamental social development which accompanies the rise of such societies is invariably limited so that the conquests achieved are of a temporary nature, and cannot be developed or permanently held. The rise of the community to impressive proportions has, in every sense, come prematurely, and the consequences are swift and merciless. So we find that the Dorylines, despite their well-developed raiding habits, their extreme excitability, and the truly immense numbers composing their communities, are yet essentially restricted to the Ponerine environments—the dense tropical rain forests of South America, Africa, and Asia, and are even more circumscribed, as a whole, than the more conservative Ponerines. The corresponding phases of human development, include, certainly, the rapid expansion of socially primitive peoples, such as the Huns and Tartars, the early Indian peoples of the Arya Decca, the early Celts, and innumerable other raiding groups in the Old and New Hemispheres, of which history has left us no record. The territorial conquests of these peoples have been of great importance. However, the ground they have gained has never been held for more than a small period of time, and has promptly fallen to the acquisitive instincts of more socially developed, expansionist peoples.

It is among the more conspicuous Myrmicines and Formicines that we begin to notice the unmistakable evidences of the coming of a totalitarian organization, with its consequent high emphasis upon vigorous and immediate mass action, and its reduction of the importance of the individual to almost nothing. And, among these giant communities of field and forest, we can detect superficial similarities to both fascism and communism.

Among humans, fascism and communism, in their modern interpretation, represent forms of totalitarianism so similar that it is difficult to distinguish one from the other, or properly to characterize either. Correspondingly, although many traits of the more socially organized ant communities are unmistakably such as appertain to a totalitarian state, their assignment as analogies to conditions of fascism or communism is not easy, and, as such, must remain largely arbitrary in character. Let us make the attempt, however, as one of interest, and perhaps worthwhile in its suggestiveness.

The treatment of the developing brood among the larger colonies of ants presents many features that are associated in the popular mind particularly with communistic human governmental forms. In contrast to the care and individualized attention bestowed by the queen and her few daughters upon her brood in the primitive ant community, the queen of the large formicary sees but a small proportion of her offspring at any time during their development. Their entire care, while actually much improved over that given under more primitive conditions, has become a routinized and standardized affair. And, since larvæ, with very few exceptions, are of no particular social value to the colony except as a potential food reserve, their treatment corre-



PRIMITIVE QUEEN-WORKER UNIFORMITY

A male, a queen, and two workers of the primitive Ponerine genus *Paraponera*. Notice how little the worker has deviated in type from the queen in these primitive giants. Sexual dimorphism, however, is already far advanced, and the male is almost exactly the type of the primitive winged solitary wasplike *Hymenopteron* (Barro Colorado Island, Gatun Lake. Photo by D. M. Gallagher.)



QUEEN-WORKER DIVERGENCE OF ADVANCED TYPE

The queen, male, and two workers of one of the highly developed species of *Atta*. This well illustrates the extreme divergence in stature and structure which has taken place between the queens and workers of some highly socially specialized Myrmecines. Notice how far the male, however, has come from the primitive wasp type toward the form assumed by the female. (St. Augustine, Trinidad, B.W.I. Photo by D. M. Gallagher.)

sponds to that status. They are handled much as are the food supplies of the colony, and their care depends entirely upon the secondarily acquired instincts of brood-nursing which are sufficiently widely distributed among all members of the colony so that the safety of the larvæ and their care by some ants are relatively assured wherever they may chance to be left in the nest. Their entire rearing, however, has become a state affair, and their education, which is apparently self-acquired very rapidly during the early days of adult life, is obtained from the observation of a large number of individuals, and is not the result of the association with a single, or a very few, preceptors.

The sharing of food—a trait carried over from early primitive colonial life and maintained essentially unchanged among the higher groups—is likewise suggestive of communistic practice. The concept of “property” seems conspicuously absent among all higher ants. There is some evidence of its presence, in relation to the much smaller brood, the “cows” and the “pets” of the socially less exuberant forms, as we have seen. The dwelling, too, in larger colonies, shows very little evidence of individualized effort in its excavation. The galleries are for the most part wide and thick, readily accessible to many ants. In the small nests of a number of *Ponerines*, on the other hand, there is a tendency to the excavation of relatively individual chambers, never occupied by more than a few ants, and connected with the main body of the colony only by narrow and tenuous galleries. Such structures are often the work of a single individual. The greatest tendency in the direction of individual construction and ownership among ants is, of course, repre-

sented by the little cell within which the young queen isolates herself.

The treatment of the injured and the sick in ant communities is of great interest in this connection. Among the primitive Ponerines, such little evidence as we have, derived largely from the observation of artificial nests, indicates that aged or infirm adults leave the colony center to die far out on its periphery, where they will never be found. This is, of course, the practice of numerous animals, and, in all probability, of many primitive human tribes to which the more advanced concepts of the mystery of death have not penetrated. Injured or dying workers of the higher ants, however, are often found within the body of the community, especially after warfare or the intrusion of a larger animal. Their treatment there is of great interest. If injured, however seriously, but not reduced in activity, at least for the time being, they are treated exactly as though normal. If they are affected in such a way as to reduce their activity, or otherwise to interfere with their social acceptability, they are avoided. If gravely injured, they are taken to the standard rubbish-heaps and thrown away. In contrast to this behavior, much consideration is shown young foraging ants, which have become lost outside the nest at some distance from it, in its immediate vicinity, or even within the formicary. Among many species, such youngsters are transported to the nest, at the end of their foraging period, by older and more competent sisters. The analogy to human behavior in the more totalitarian states is obvious and interesting.

Common to both forms of totalitarianism in its analogy, is the almost complete submergence of the importance of the part played by any individual in the

community as against the integrated activity of that community as a whole. Such activity inevitably accompanies the development of complex societies among ants. Many individual workers of the Attine colony and of the huge colonies of the grain-harvesters and of other similar communities, may disappear entirely, may cease working, or may modify their behavior profoundly without producing so much as a ripple upon the placid social surface of these stably constituted super-organisms.

Some other features of the highly organized ant societies are much more suggestive of the development of the fascist type of state. Such, especially, is the role played by the queen in the social lives of the larger ant colonies which, throughout their corporate existence, recognize only the queen which gave them birth. The queen, in such communities, is sharply differentiated in form, in function, and in treatment, from her workers. This is in contrast to her position among the primitive democracy-types, where her functions and the attentions bestowed upon her differ but little from those of her grown daughters. The resemblances of the queen of the large ant colony to the dictator of the fascist state are as striking as the differences, which we shall later consider. The state has come into existence by virtue of her existence in it, and its continued existence is in very large degree dependent upon her continued presence. The same may be said of the dictator of the human fascist state. The queen ant is the center, wherever she moves in the colony, of a concerted, highly "mechanized" attention that may reach exaggerated proportions, which again is highly reminiscent of fascist conduct. The downfall of the state normally ensues

shortly after the downfall of the predominant figure within it, and its activities during her lifetime may be profoundly modified by her behavior. Her periods of activity and rests, her ovulation cycle, and her degree of fecundity all affect the day-to-day actions of the colony. So also, the first location of that colony, with all its implications, represents the direct choice of the young queen-mother.

The treatment of the queen in death in these giant communities is as distinct as that accorded her during her lifetime. Whereas the dead or dying workers are indifferently thrown aside, the body of the deceased queen may be retained, carried about, and treated with the most marked attention by the colony so long as it remains recognizable. The behavior of the colony is modified when its center is gone. From an active, expanding, aggressive community, it becomes changed into an increasingly timid, placable group, which finally melts away into a disorganized band of workers that diminishes in size as its components perish of old age.

Typical of advanced social development, but by no means always comparable with governmental evolution in human societies, is the development of the remarkably rigid caste systems among the higher ants, which even today lacks a satisfactory biological explanation. As we have seen, extreme specialization of social function accompanies specialization of structure—and is often, indeed, necessitated by it. So, similarly, do the mental specializations of human populations necessitate specializations of function. The puzzled youngster, for example, endeavors with might and main to enter that line of activity for which his already definitely formed mental equipment best fits him.

Vigorous expansionism is a feature characteristic of the ant, as of the human, totalitarian state, and is probably in both cases a reflection of the greatly increased margin of social vitality which highly developed social forms have made accessible to the community. Aggressive warfare against neighboring communities, usually undertaken for the possession of land and food supplies, is a constant activity of the more highly evolved ant colonies, and we shall in another chapter consider at greater length the campaigns of world domination which have been undertaken, more or less successfully, by several species. Invariably, the types of ants that habitually exist in populous and closely knit communities are the ones to be found occupying the most desirable geographic situations, and which control the most available and abundant food supplies. They control these supplies to the extent of utter domination until, with the development of internal difficulties, with the growing demands of parasites and pets and other colonial luxuries, they are forced to relinquish their holdings to other, less harassed groups. And it is these ants which, as a whole, have fallen heir to the world. They are to be found wherever man exists, and in many parts of the globe not ordinarily inhabited by him. They are denizens of the high mountains and the deep valleys, the open plains and the dense forests. In the parts of the world in which the struggle for existence is keenest, they alone can live and contend among themselves for the possession of the richest territory. In the benigner parts of the globe, amid heavy tropical forests, or on isolated islands and peninsulas, they share the land, when they must, with their neighbor, primitive ant democracies. But the association is an unwilling one, and it will persist

only until some slight shift in environmental conditions favors the populous colony. Then begins the long, slow, relentless drive to exterminate the group in which the activity of the isolated worker is still an important factor. Such a drive goes on today in the Bermuda Islands between two rival communities of these sorts, and a similar fierce battle was fought a decade ago for the possession of Madeira. These things we shall consider in another chapter.

The evidence of the ants confirms for us the conclusions that the study of mankind seems to make almost inevitable. The democratic form of state, with its emphasis upon the activity of the individual, its reliance upon private enterprise, and its relatively poorly developed systems of communication and coöperation from individual to individual, represents a primitive social condition, characteristic, on the whole, of the youth of a race. Totalitarian societies, with their negation of individual freedom, their development of arbitrary concepts, the rigid enforcement of their wills by means of closely concerted actions of the members of the societies, their resultant social vitality, and their collective pugnacity and expansionism, are undoubtedly complex, advanced forms which appear late in the history of a culture. As a culture matures and approaches old age, the totalitarian form more and more completely replaces and dominates the democratic types characteristic of the middle-youths of nations. Ultimately, by virtue of its greater social competence, it displaces the democratic type, only itself to decline, a prey to social senescence.

Herein is shown the enormous difference in the ages of the societies of ants and of men. Among ants, with their social origins lying in Tertiary times, the totali-

tarian state has become the dominant one, and has left its democratic remnants only as archaic survivals. Here, too, the bad effects of senescence, slaves, pets, and parasites are all too evident among some of the societies in which the totalitarian structure is very well developed. The case with man is very different. The democratic form of social structure, with its emphasis upon individual initiative, has, in the large, been the dominant one in motivating his development. The totalitarian experiment has been furtive, and short lived, and has in nearly every case appeared at the maturity of a local culture. Totalitarianism dates back for many thousands of years, but at no time has there been evidence that mankind has become sufficiently socially mature for such a system to be naturally accepted by it, and it has never proved naturally dominant, as it has among the ants. The evidence still indicates that the totalitarian state is too immature to be anything more than a local development, and that it is poorly fitted to be imposed upon a culture which as a whole has hardly outgrown its early youth. The question before us, then, is really that of the stage at which mankind as a whole will reach that degree of physiological maturity at which totalitarianism, the mark of social prime and decadence, will become generally applicable. And that question only the future can answer.

It is important to notice that the parallels which have been drawn only emphasize the common mold into which two fundamentally different societies have been poured. There are wide differences, of course, in the structures of the societies of ants and men, and in the means by which their common ends are achieved. Most striking among these, perhaps, is the complete lack of

any sort of conscious direction of one individual by another, as we understand it, in ant society. The best-coördinated ant society is bound to its social pattern by the operation of complex patterns of instinct and of learned behavior.

So far as we can at present ascertain, ants adjust themselves to social living and carry out complex social processes primarily as a result of forces arising within each individual separately, with very little emphasis upon instruction, which plays so dominant a part in human society. Coercion, in fact, is essentially unknown in ant society, for the colony, as it stands, is a selected group of individuals which tend, purely as a result of their own structural characteristics, to remain in that state. Any "antisocial" individual is free to wander away from the colony and never to return. This is the normal course of the asocial males, and it is a course frequently pursued by workers of the more primitive *Ponerines*. It is also, of course, the normal behavior of the young queen. The condition which pertains among human societies, in which the will of a small group is enforced upon the remaining population, is unthinkable among ants. In this respect the societies of ants are far more perfect as social organizations than those of men, and represent a more specialized condition, for the will of the society exists in each component of it. The emphasis which is placed upon brain activity in human societies is shifted in ants, to a great degree to physiological activity, which operates through the binding ties of trophallaxis and other brood relations, as we have seen. This is not to imply, however, that the force of instruction is entirely absent. Every ant which carries another to a source of food, or returns home with it at night,

and every colony which is shifted by a few enterprising members which carry their fellows to a new location is practicing communication and instruction of a very definite sort. So are those ants which, by means of their stridulatory apparatus, assemble their fellows around some food or other cause of excitement, and so, too, are those arboreal tropical ants of the genus *Camponotus* which signal from tree to tree by tapping the bark and leaves so vigorously as to produce a sound like falling rain. Some sort of communication and precept undoubtedly guides the columns of slave-raiding species of *Formica* and *Polyergus* to the nest-sites of slave species, discovered perhaps days previously by a few straggling scouts. But these devices, simple and mechanical by comparison to those employed by humans, play but a small part in maintaining colonial solidarity. The part taken by human regulations, constitutions, laws, and law enforcement, is played among societies of ants by social ties that are heeded by every participating member of the group—else it ceases to be a member of that group. And so thoroughly has the social behavior pattern become fixed in these creatures, so socially ancient by comparison to ourselves, that a complete lack of any sort of coercion, among the higher ants, results in the loss of so few “antisocial” members as to leave the strength of the colony virtually unaffected. Similarly, the social forces are so strong in the colony that behavior contrary to the social interest (so long as the colony has been maintained under normally balanced conditions) is almost unknown.

Yet if the trophic balance of the colony be upset, by removing it from its normal nesting site, by changing its food supply, or by radically altering the numbers

of its personnel, antisocial behavior may arise among large numbers of the workers, and is carried on without protest from any member. Slaves will often kill their mistresses in slave-holding colonies in artificial nests, or will withhold food from them until they die. Males and young queens may be killed and devoured within the nest by their own brood-sisters. Cocoons are cut open and the developing pupæ slaughtered and thrown on the rubbish heap, even when the murderers are themselves not hungry enough partially to devour them. And all of these things may be brought about under perfectly natural conditions when forces operate to destroy the balance of the colony. Pets and parasites, when they become dominant and overbearing in the colony, may completely upset its economy, and will be encouraged to do so by the ants themselves. Slave species and the temporarily and permanently socially parasitic ant species destroy the domestic economy of their hosts, so that the latter may at times spontaneously kill their own ruling brood-queens, as we shall see in another chapter.

Consonant with this condition is the fact that the queen of the colony, although very like the dictator of a totalitarian state in her social effect upon the group, achieves that effect by an entirely different mechanism. She is in no sense a "mental" director or guide to her colony, and wields no "authority" whatever within it. Whatever effect she achieves—and it is vast—is accomplished wholly by the actions of her workers, and by links almost purely physiological. Nevertheless, it is interesting to notice that the position of the dictators of totalitarian states may at times approach rather closely to that of the queens of the larger ant colonies. Thus,

the passionate enthusiasm of a hysterical mob for a national hero may for days be governed by motives not too different from those governing the attention paid the queen. The queen and the dictator may both, for the time being, function almost passively, and may stimulate the reception of extravagant ceremonial attention by their mere vegetative existence. Too, they may have little or no control over the forms or the extent of that enthusiasm.

Finally, the attitude of adult ants toward their young must in the nature of things be different from that obtaining in human groups. The young adult ant is of the same form and general habits as its elders, and its relationship to them approaches, to some degree, that of the student entering college to his father. As with the student, some aid must be given from time to time by elder relatives. The young insect may be carried to a new nesting site, or brought home in the evening when it has become lost during foraging expeditions. But in general, its learning and the development of its behavior pattern, which are usually achieved in the course of a few days, show far more self-help than those of the college student, or even the graduate. So far as we know, the young ant receives no systematic instruction of any kind, and its rapid learning is almost completely the result of observation and imitation undertaken on its own initiative. So much for the parallel of the ant and the human adolescent.

When we come to our babies and young children, for whom intensive systematic instruction is undertaken far more intensively and carefully than for their older brothers and sisters and whose learning is much more rapid and varied than in later years, we have no parallel

whatever among ants. Their young at this stage are radically different from themselves, and there is no possibility whatever of sympathetic attention. They are either wholly insensitive and passive eggs or pupæ, or they are irritable but alien larvæ—as unlike their parents in form and function as the tadpole is unlike the frog. Their chief interest to the ants lies in the exudates which they produce. Their relationship to their nurses, throughout their immature life, is much more like that of an animated food supply than like that of young, learning members of society. It is this resemblance to an animated food supply, in fact, which seems first to have led to the institution of slavery, as we shall elsewhere see. Consequently, so far as any training or the possibility of any similarity of outlook is concerned, the opportunities of the young ant are entirely confined to its few callow days after pupal emergence, and even then its deliberate training is of the most casual sort. And yet that young worker, on becoming adult, will be as perfectly fitted for its social existence as any member of any society that we know—far more so than are the great majority of human beings for the societies of the cities of today. Where else can we find evidence of a society so perfectly constituted, the basis of whose social adjustment is removed from the mental sphere?

It seems evident that ants have passed through the primitive hunting stages of social development into early, democratic states, and from these, again, into a condition resembling totalitarianism, which prevails among the great majority of them today. Their course would seem to confirm the current concept that, among humans, totalitarianism is indeed the more recent, and, from the standpoint of group efficiency, the more ad-

vanced, social form. It is also closer to social decadence, as a study of both ant and human social groups will amply confirm. The parallel, however, is not to be pushed too far. Ants are so much older than humans in their social development that their present state may well represent the final inevitable outcome of evolution, but not the most desirable state, for man. Further, the very structure of ant society, with its specialization of the reproductive function in one or a very few individuals, tends to encourage totalitarianism, and probably brought it earlier in social evolution than it has, comparatively, come for man. Even among the most primitive of ants it is foreshadowed, as soon as the division of reproductive labor between queen and worker has taken place. Mankind, fortunately or otherwise, has preserved intact one of its greatest physiological guarantees of democracy—the general distribution of reproductive capacity among all members of its society. Yet, as a social device, this is a highly inefficient one, and even today we see many evidences of the beginning of its abandonment. How often do our sociologists lament the low birth-rate among the most socially useful of us, the highly intellectual group! How often is it said that our race is speeding to destruction because its brains are consistently bred out of it, while the ranks are kept full of the descendants of those who, because their energies are turned into socially less productive spheres, are more active in the reproductive one!

Yet we find little diminution in the number of socially productive individuals in each succeeding generation. Within those human societies which have slaughtered their intellectuals of any one generation as a result of internal political dissension, the gaps in the ranks of the

intellectuals have been filled within another hundred years, from descendants of the socially less useful people who survived. The evidence seems to be that a mentally gifted population can spring at any time from a less highly gifted, earth-living substratum, which can take their production as its main function.

Today, the most outstanding members of our society are characterized by attempts to succeed brilliantly in both social and reproductive spheres, and the combination of effort imposes a strain upon them which is unduly rigorous for all except the very hardiest, and often shows itself in an inferior social and bodily endowment of the succeeding generation. Whether a split will eventually occur about this social dilemma, whether human societies will ever follow the course of the communities of ants in their social growth, and rigidly separate and specialize, some in the social and some in the reproductive functions, in the interests of community solidarity and efficiency, only our descendants of future millenia will know.

Wa

WHENEVER a social group has become so efficiently organized that it has gained access to an adequate supply of food and has learned to distribute it among its members so well that wealth considerably exceeds immediate demands, it can be depended upon to utilize its surplus energy in the attempt to enlarge the sphere in which it is active. This condition, of course, parallels that of any growing organism, and it inevitably leads to expansionist policies. Expansion may be internal, as in the democratic human states and in very loosely-knit colonial organizations among ants, wherein the "interstices" of the social structure, so to speak, are large enough to permit considerable growth without the resistance of external pressure. Among more closely-knit societies of ants and men, however, this opportunity for internal growth is absent, and the only alternative is the subjugation of additional territory as feeding ground, and, at times, the domination of other organisms to aid in the program of expansion.

The structure of ant colonies renders them particu-

larly prone to this sort of expansionist policy. With very few exceptions, ants of any given colony are hostile to those of any other community, even of the same species, and this condition is bound to produce preliminary bickering among colonies which are closely associated, even when they are very young. Beautiful examples of this sort of thing can be seen in the tropics among ants which habitually nest in cavities of plants, such as the ants of the genus *Azteca*, which nest in the hollow twigs of trees of the genus *Cecropia*. While the trees are quite young and inconspicuous members of the forest, their older twigs are entered by numbers of young, newly deälated queens of *Azteca*, seeking convenient and secluded spots in which to begin their colonies. The branches of many species of *Cecropia* are by habit spongy in the interior, but are supported at intervals by more solid woody septa. The young queens hollow out the pithy portions to make their chambers, but leave the septa intact, thus isolating themselves from one another. This condition suits their purpose well, for, with very few exceptions, young queens dislike one another's society after the marriage flight, even though they be from the same colony. They are far from aggressive, however, and their natural inclination, when thrown together, is merely to build up walls between themselves. This represents the only truly tolerant phase in the life of the normal ant colony. Numbers of *Azteca* queens may come thus to reside side by side in a young developing *Cecropia*. Although they live in close proximity to one another, they have no communication. To all intents and purposes they are completely unaware of one another's existence.

This condition is too good to last. Young first broods

of workers shortly come to maturity in each of the incipient communities, and perforate the walls of their homes to obtain egress to the surface of the twig. Their business in life is to bring home as much food as possible from the outside world. In this effort, all the workers of all the colonies are immediately brought into sharp competition for food sources, and the members of each colony are implacably hostile to those from any other. This condition shortly leads to much individual combat and the loss of very many workers, to the detriment of the growth of all the colonies. If the colonies be numerous, and of about the same age and strength, minor conflicts of this sort may persist for a long time, and the development of all the groups be seriously affected; for at this stage the loss of a single worker is a tremendous disadvantage to colonial growth. No one community will dare to invade the nest-chamber of another, because their relative strength is so nearly equal as to make the undertaking a highly hazardous one.

Eventually, however, as the *Cecropia* tree grows and emerges into the sunlight, as the number of its branches increases, as the foraging space upon it expands and the quantity of insect life parasitic upon it and available to the *Azteca* ants as food becomes greater, the condition of equilibrium in strength among colonies is bound to be disturbed. Some one or two communities become more favorably situated than the rest with respect to food supplies, and the numbers composing the groups increase correspondingly more rapidly. Pressure for room is felt by the fortunate colony in its narrow internodal chamber, and, emboldened by its increased numbers, it perforates the septum which sets it apart from its neighboring community. Immediate warfare ensues, in

which the entire colony participates, and there are usually very considerable losses on both sides. Ultimately, the weaker colony is forced to flee the site and to seek dwelling elsewhere, usually entirely off the tree. With it will be carried such of its young as its surviving members can transport. The rest, abandoned in cavities of the deserted nest, will be found by the invaders. The young of alien colonies of ants are usually accepted and adopted by other members of the species, so these are quite likely to be added to the brood pile of the invaders, to swell the numbers of their next developing generation. The adopted insects, since their whole learning period as young adults will be spent in the company of the invaders, will become loyal members of their foster community.

The invading colony now settles in its new territory, re-excavates it, redesigns it to suit its own ends, and proceeds as before. Expansion of numbers is now quickened by the new opportunities for food-gathering which its conquest has brought. Later, the pressure of numbers is again felt, and the colony undertakes the raiding of a third community of its neighbors, with results similar to the second raid. The new territory, food-supply, and breeding and foraging grounds are appropriated in the same manner. In the meantime, similar strife has been going on among local neighboring communities on other parts of the tree, resulting in the selective elimination of all but a very few colonies. The interval between wars is longer now, for there is more room for development, and warfare, among ants as among men, is rarely undertaken for the fun of it. However, it is inevitable that the few remaining colonies, now enormously strengthened in numbers, should come into intolerable rivalry.

The campaigns are now on a very much larger scale, are more elaborately carried forward, are more boldly waged, and last much longer. Finally, however, a single community will win and will dominate the entire tree. By the time the *Cecropia* has attained a large stature, it will be completely controlled by one colony of ants, and life for any alien upon it will be made so unpleasant that henceforward no young queens will attempt to start colonies there, and ant communities of other trees will not find it worth while to attempt campaigns there. The domination of the world, so far as the world lies within the ken of *Azteca*, has been completed, and henceforward a totalitarian state pursues a peaceful course, up to the point of its ultimate dissolution from internal causes.

The course of the conflicts just referred to is characteristic of the wars of the majority of ants. It is equally characteristic of the soil-nesting species which occur about our homes, although here the greater opportunities to find food, while avoiding neighboring colonies, allow stronger communities to coexist near to one another. However, the raiding spirit may be emphasized in many ants, to the extent that they become habitual pillagers of the colonies of aliens. In such cases, they quickly rob the domicile and as quickly depart, making no attempt at a permanent occupation. This habit is widely distributed among ants in general, and is particularly characteristic of the first of the slave-makers.

Such colonial warfare finds innumerable parallels in human society. It is especially characteristic of early tribal life the world over, and every young culture is featured by tribal wars similar to the intercolonial wars of young ant communities. So far, however, we have

presented no analogue of the large-scale warfare which occupies mankind in its maturer years.

Before large-scale warfare can appear among ants, it is necessary that some sort of coöperation be exhibited between neighboring colonies of the same species. For the biological structure of ant society presages that the numbers of any single group must be limited by the fertility of one or a very few queens, and single colonies cannot hope to be great enough to accomplish any sort of world domination so long as they are without allies.

The first step in the changing of this condition is to be seen among certain rather benign earth-loving ants of the Formicine subfamily, notably in the genus *Acanthomyops*. These ants possess a very strong odor, so pronounced as to be readily sensed by human beings and to possess a marked resemblance to oil of citronella. Perhaps because of the strength of this odor, the far more delicate, presumably odoriferous, differences between ants of different colonies of the same species are not perceived. In any event, it has been noticed by many observers that differing colonies of this insect rather readily and peacefully fuse to form super-communities. This fact can easily be checked by any reader, since the ant is commonly found about many houses and gardens. Fusion results in the formation of a peaceful, giant community, and has very little if any effect upon the expansionist policy of the group. These ants are slow-moving and subterranean, largely vegetarian in habit, and are in the pastoral stage of development. They keep great numbers of root aphids, which are carefully attended, and whose cultivation provides a satisfactory store of nutriment in a restricted feeding territory, and absorbs so much of the energies of the nurses that little

effort is spent in acquiring more than a modest portion of soil, considering the size of the community. The tendency of these ants to mix with one another is of great significance, however, for as soon as any species of ant acquires the power to form a large state of ants of that species, its power of world domination becomes very greatly increased.

Pheidole megacephala is a small yellow Myrmicine ant, now known in the tropics around the world. The ant possesses the sharp differentiation into soldier and worker castes characteristic of its genus, and is distinctly aggressive. It appears originally to have been a grain-harvesting species, at least in part, like so many of its allies, and the structure of the mandibles of the soldiers, admirably fitted to act as crushers for hard objects, is still retained. In times of need it reverts, even today, to its ancient habits. Its original home was in the tropics of the Old World, presumably in some relatively dry region in which its grain-harvesting habits would be of particular value. The island of Madagascar seems its most likely homeland, since the greatest numbers of its varieties are found there. *Megacephala*, however, seems to have been characterized by a degree of energy, as a race, and a degree of acuteness, as an exploiter of its environment, which are astonishing. Within the last century it began a campaign of exploitation which has left it racially predominant in the tropics throughout the world. This is a very different sort of conquest from the simple colonial warfare which we have surveyed, and is worth careful analysis.

Abandoning the seed-harvesting habits which have for thousands of years been characteristics of its genus, *megacephala* took up two new habits which have been

of tremendous significance. It began to cultivate aphids and other coccids, thus reverting from an agricultural to a pastoral existence, and it became adapted to nesting in ships and other conveyances used by man. While it retained its ability to survive in dry areas, it sought environments, such as man-made structures, which were practically free from the social competition of other species. Once it had undertaken the role of the house and ship ant, it was literally transported to the ends of the earth. It was introduced into many islands of the Atlantic and Pacific, and proceeded in its conquest in a very definite way. We have a particularly good picture of the way in which this happened in Madeira, thanks to the observations of Heer.

Pheidole megacephala apparently came into Madeira early in the nineteenth century. At first it confined its nesting sites and its foraging activities almost wholly to the houses and gardens of the settlers, where food was abundant and the competition of foreign species small. New types of bulbs and other plants appeared in the settlers' gardens, and before long they became infested with aphids and such sweet-excreting insects. *Pheidole* promptly took charge of these insects, encouraged their increase, and fed largely upon the manna which they produced. Gradually, as the pressure within its own species increased, and as the native ants weakened with the advent of man, *Pheidole* pushed back into unsettled territory. It first established itself in the bleaker, less hospitable regions of the Island, in which it alone was fitted to survive. With these regions as a base, it shortly raided more attractive ground, and began a steady, deadly push against the less hardy, less adaptable, and less organized types. Mass raids are the rule with *Pheidole*,

and hosts of the tiny creatures evidently invaded nest after nest of larger but more loosely organized species, killing the queens, and forcing the workers to evacuate. Their own losses in workers were terrific, but the great fecundity of their queens maintained the pressure of numbers, and the race pushed onward. When Heer visited Madeira in 1852, no species of ant save *Pheidole* could be found. It had occupied every crack and cranny from the shore line to the highest crest of the Island, and had become a serious house pest. Outdoors it fed on dead insects, occasionally on seeds, and cultivated aphids and other forms of nectar-producing insects. Indoors it abandoned every form of raiding and cultivation and subsisted quite simply on human food stuffs.

Once the conquest of the Old World was fairly under way, *Pheidole* crossed the Atlantic and established itself in various places in the West Indies and elsewhere in the New World. And here it may now be seen in the process of establishing its conquest. The Bermuda Islands, in 1929, were rather extensively occupied by a handsome species of *Odontomachus*, known as *Odontomachus hæmatoda*, var. *insularis*. This genus of ant represents one of the most active, resourceful, and aggressive of the Ponerines of today—one of the very few which is in any sense dominant among modern ants. It is probably of relatively recent origin among Ponerines, as the evolution of that ancient subfamily goes, and is distributed, in one species or another, around the world, *hæmatoda* being especially widespread. The ants are large, active, and aggressive, and in all probability represent the remains of a fauna which was nearly dominant among the Ponerines in late Tertiary times. Individually, it is far superior in size, strength, and sense-organs to *Pheidole*.

Its colonies, however, although large and closely-knit for a Ponerine, are still far inferior in numbers and powers of coördination to those of the tiny *megacephala*. In 1929, *Odontomachus* was quite abundant on the higher parts of the main island of Bermuda, nesting particularly under stones and logs in the rich, grassy vales of the cedar groves. Along the shore line, existing in the most inhospitable situations in shifting sands and between blocks of coral, almost exposed to the salt spray, were numerous active communities of *Pheidole megacephala* which had probably come on a ship not long before. Today *Odontomachus hæmatoda* is almost extinct in its former haunts among the cedars, and instead *Pheidole* colonies are to be found in every patch of sod. In the few *Odontomachus* colonies remaining on the Islands great numbers of *Pheidole* workers are to be found killing and carrying off the larvæ, fastening themselves in myriads to the bodies of the workers, and forcing their early abandonment of the site.

Within another ten years, the Ponerine species, which has inhabited Bermuda as its undisturbed Arthropod mistress for millenia, and has in fact developed a characteristic variety there, will have been exterminated. Such are the powers which lie in close social organization and large-scale concerted action among ants, as among men.

Pheidole megacephala, while far inferior in strength and senses, as an individual, to *Odontomachus*, is much superior in organization. It is, however, a Myrmicine ant, and, as we have seen, the Myrmicine organizations are excelled as a whole by those of the Formicines and certain Dolichoderines. This is true of the Dolichoderine genus *Iridomyrmex*, and a species of this group,

humilis, recently undertook a drive for world domination which has been even more striking and successful than that of *Pheidole*.

The workers of *Iridomyrmex humilis* are tiny, soft-bodied, dark-colored insects of extremely active, nervous habit. They are somewhat smaller than the workers even of the tiny *Pheidole*, and, instead of being protected by a heavy chitinous armor, they are very fragile and easily destroyed. Unlike *Pheidole*, they have no sting whatever, and the only means of individual defense which they possess is a white, sticky secretion which can be emitted from the anal glands, but which is of very dubious value as a weapon. Altogether this creature would seem much less able than *Pheidole* to cope with the world. *Humilis*, however, possesses certain social advantages over *Pheidole*. The members of its colony are more closely coördinated than those even of *Pheidole*. They habitually forage in column, and their sensitiveness enables them to exploit new advantages more readily than the more stolid Myrmicine. Of particular advantage to them is the distribution of their reproductive function. *Pheidole* has retained the ancient Myrmicine habit of rearing very large, bulky queens, expensive to produce and to maintain, but well adapted to the foundation of colonies in the classical fashion. Consistent with this behavior-pattern is the fact that individual colonies of *Pheidole* ordinarily recognize only the single queens which founded them. They are therefore highly vulnerable, for it is only necessary for an invader to slaughter this single queen to cause the destruction of the colony. *Iridomyrmex* has remedied this condition to a remarkable degree. The queens of *Iridomyrmex* are tiny, soft-bodied, and active,

but little larger in stature than the workers. Very many are permitted to coexist in a single colony. Queens of this type are easily and inexpensively reared in large numbers. They are, of course, unable to found their colonies in the ancient, independent way prevalent among most ants, but this method is no longer necessary under the new living conditions of the *humilis* community. Instead, colonies of these ants bud and divide again and again, each new division taking a few queens with it, and thereby rendering itself nearly impregnable against extermination. The old division of colony from colony, so long prevalent among ants, has nearly been broken down, and a world-state of a single species, through which queens may be uniformly distributed, is being substituted.

Armed with these social weapons, *Iridomyrmex humilis* a few years ago undertook a campaign of expansion which has left almost no part of the tropical world which is inhabited by humans unknown to it. Its original home seems to have been Argentina. Like *Pheidole*, it became an adept at living within houses and ships, and has made extremely good use of man in extending its range. It apparently entered the United States at New Orleans several years ago, and thence has spread eastward and westward along the southern tier of states until today it is known and detested from Florida to California. It has crossed the Atlantic and has appeared in such widely separated localities as Portugal and Cape Colony. It has arrived and established itself in Sicily and in southern Italy, about Naples. It has infested the Canary Islands, and has made its appearance in France and in the vicinity of Hamburg in Germany. More clever than *Pheidole* in taking full advantage of human

habitations, it has used them to extend its climatic range, and has established itself in Guernsey and in various parts of the British Isles, even penetrating as far north as Edinburgh. Considering the size of the organism, its colonizing travels and conquests, which have carried it from Argentina to England, and south and eastward into Asia within a period of little more than fifty years, are impressive indeed.

Madeira is a crossroads for the traffic of the South Atlantic, and as such it could hardly better be missed by *Iridomyrmex*, coming from the western New World, than by *Pheidole* in its march from the East. Accordingly, the former arrived some time between 1852 and 1898, and immediately came into conflict with *Pheidole*, which had by 1852 exterminated all of the native ants of its environment, as we have seen. Nowhere could a better theatre of action have been found for the observation of this conflict of two world-conquering races. Proceeding by methods almost identical with those employed by *Pheidole* on the same soil a half-century or less earlier, but undoubtedly with the superior strategy born of its more complex organization, *Iridomyrmex* completely displaced the earlier invader, and today Madeira is overrun with the foraging columns of the tiny brown "Argentine ant" pest, while the *Pheidole* colonies of yore are not to be found. The conquest is complete, and the relative merits of this Myrmicine and this Dolchoderine ant as world-conquerors have been determined for all time.

The analogies to human behavior in the local wars and the general wars of conquest of ants are numerous and obvious. Small tribal warfare and general wars of replacement have featured human history ever since

society became complex. The analogies in these cases, moreover, seem to be real throughout, and do not require the qualifications expressed in the last chapter. This is true, of course, because the fundamental aims of conquest—increased food and shelter—are identical for ants and men, and the means of obtaining them are similar for both races.

It is less easy to see among ants than among men why some races should suddenly take up an expansionist policy, and shortly come to dominate very large tracts, when hitherto their existence had followed the same quiet pattern as that of surrounding related groups. *Pheidole megacephala* is but one species of a huge, structurally homogeneous genus that is rather thoroughly distributed over both hemispheres. Why should it alone, of all its contemporaries, suddenly have abandoned the traditional, peace-loving, grain-harvesting mode of life, and become extremely fecund and aggressive?

The genus *Iridomyrmex*, and the allied genus *Tapi-noma*, contain many species of closely similar insects, all of whose opportunities and excuses for world expansion would seem to be as obvious as those of *humilis*. Yet no one of them has behaved in a fashion even remotely similar to its brilliant and dramatic, if destructive, relative. We are faced with exactly the same problem among humans, of course. Historians and anthropologists are today at a loss satisfactorily to explain the waves of Celtic migration into Europe from the East, or the whirlwinds of discontent and migration that anciently took place on the plains of Arya Decca. They are helpless in the face even of such recent events as the tempests of the Far East which ultimately drove

the Huns and the Visigoths across the Rhine, which they were not audacious enough, at the fall of the Roman Empire, to dare to cross, had they not been motivated by terrific pressure from the rear. Neither do historians understand the causes which drove the raiding Iroquois from their homes in the Ohio Valley to the eastern coast of North America and transformed them from a hunting to an agricultural people in the century before the arrival of the Puritans. The sudden vigor which motivates a race to sweep all others before it in its dogged determination to increase its own sphere is difficult to understand. Such vigor often does not come to the nearest relatives of the conquistadors. We know only that such waves are invariably and necessarily followed by the formation of a super-state, in which tribal or colonial boundaries are temporarily broken down, among men as among ants. The beginnings of such movements among men are almost always shrouded in obscurity. All of them took place at a remote period, as men count historical time, and they cannot be repeated in their typical form under our present conditions of civilization. Consequently our opportunities for the gathering of evidence concerning these strange movements among men are probably exhausted.

The case is better among ants, and in this field of social study particularly, the Formicids would seem to hold out, as the reward of painstaking sociological investigation, prizes of the richest character. Interest in their attempts at world-expansion should be centered particularly about the beginnings, where the causes should be ascertainable by observation, if anywhere at all. This is precisely the period of the movement, however, which usually goes unnoticed. No one knows how

or where, or under what circumstances, *Pheidole* or *Iridomyrmex* took up the habits which have resulted in their startling achievements. Yet these modifications must, in the nature of things, have been made not only in historical, but in recent, times, and directly under the eyes of many men. But at that time these were but inconspicuous ants of the fields, unworthy of any special attention. That attention was not given them until after the completion of their designs. In the same way the beginnings of the most significant human movements remain unnoticed until their culmination has been reached, and our knowledge of the causes of most important human events is woefully inadequate.

If it should fall to the lot of any student of the societies of ants in future years to detect a movement for world expansion in any species at its inception, and to follow its growth and development through to the end, he would be able to give to the world its first consistent account of a phenomenon of this kind. He would contribute information which could hardly fail to be of the highest value to the historian and the sociologist, which should be of great interest in interpreting numerous phases of the past of the human race. The investigation of such a movement, moreover, could well fall in its entirety within the life of a single observer; for the whole dramatic expansion movements of *Pheidole* and *Iridomyrmex* were substantially completed within fifty years of the time that they first were noticed. And, if the experiment be artificially conducted with one of the two species known to possess these tendencies, and the theatre chosen be an isolated oceanic island or island group, a careful investigation could even now be run through within a very few years, and the

information so gained should be of immense value. Let us hope that some sociologist who is concerned with ants or men (it makes very little difference which) will have the fortune to undertake such a task in the near future.

Slavery

WE HAVE SEEN that one consequence of colonial warfare, conquest, and expansion may be the temporary breaking of intercolonial barriers and the establishment of world conquest by the resulting super-colony of a single species. Strikingly enough, another end of the same movement seems to be the establishment of the institution of slavery, with its succeeding degeneracy of the slave-makers, and, possibly, the ultimate disappearance of the worker caste among them. Likewise, the institution of temporary social parasitism seems to be associated with the beginnings of slavery. We have seen in an earlier chapter that the queens of certain ants have abandoned the classical mode of colony formation, in which the colony is built up solely from the tissues of the isolated young female, and have instead sought adoption in young and weak communities of other species of ants. In the more primitive stages of this development, the queen and the young brood of workers of the invaded colony are assassinated by the intruder, and the developing brood is adopted. All of the slave-

keepers known to us follow this practice in the establishment of their colonies.

We have seen how closely associated the obtaining of food is with the care and nurture of the young ant brood. The young colony of our last chapter, which raided and invaded sister communities in order to decrease competition and increase its own foraging ground and incidentally carried off the young larvæ of the defeated group, needs to take only a short step to undertake such raiding for the sake of the larvæ to be gained rather than for territory. Larvæ at all times represent a stable food reserve for the colony possessing them, and, for an aggressive, bold species of ant, one of the easiest food sources obtainable is the brood of other ants. Accordingly, we find many species which have become habituated to raiding the nests of other ants, and to carrying off their young, and which do not trouble themselves to drive their adult victims from their haunts, nor to occupy their strongholds, since their own territorial aims are already satisfied.

Typical of this group is *Formica rufa*, the "horse ant" or "fallow ant" of England and Europe, whose great thatched mounds form a conspicuous feature of the German forests. *Formica rufa* seems truly to represent the beginning of the slave-making habit. It habitually raids the nests of other species for their brood, which is brought home and devoured. Huge piles of alien young are often accumulated within the nest at one time, and these are eaten gradually, as necessity develops. It sometimes happens, however, that a few of the stored young reach maturity before they are devoured. Under these conditions, they emerge into a colonial existence very like their native one, become swiftly adjusted to it

during their learning period, and are accepted and adopted into the colony. They function as helpers throughout the remaining life of the community. They are on the whole less valuable than would be an equivalent number of *rufa* workers, since in general they have been recruited from less powerful and less able species of *Formica*, but their presence is an asset rather than a liability to the colony, and they are allowed to remain with their adopted foster-parents throughout their lives. The young queens of *Formica rufa*, after their marriage flight, either secure adoption in a populous formicary of their own species, thereby swelling its reproductive capacity and prolonging its life, or they attack a very young colony of a weaker species, rob it of its brood, and bring up the young aliens. These promptly behave as they would toward their own mother, feeding her, and receiving and caring for her eggs and rearing her young. Within a short time they, not the young queen, have brought to maturity a brood of young *rufa* workers. The young *rufas* at once take over colonial duties, and the alien species, now definitely unnecessary in the social economy, gradually dies out, leaving a pure *rufa* colony, which may become very powerful. Both of these peculiar habits of *Formica rufa* apparently represent important bases of the slave-holding habit in ants.

The next stage is best represented by *Formica sanguinea* and its subspecies—the large, red-and-black ant which builds mounds in conspicuous positions in the fields and woodlands of temperate America and Europe. The queens of *Formica sanguinea*, like those of *rufa*, found their colonies by pillaging incipient communities of weaker related species, and robbing their young. All of the young colonies, therefore, are composed of a mix-

ture of the two species. In a number of subspecies of *sanguinea*, subsequent colonial behavior is essentially like that of *rufa*. Larvæ and pupæ are taken as food from pillaged communities throughout the life of the mother colony, but only rarely and sporadically come to maturity within the groups. Under such conditions, the young of a wide variety of species may be taken and devoured.

Among other subspecies of this ant, however, a significant change in behavior has taken place. The young that formerly were captured to add to the food supply, and only accidentally came to maturity within the colony, are now deliberately obtained and reared for the purpose of artificially increasing the size of the community. The slave-making habits of the queen become manifest in her daughter workers, and they keep up and increase the supply of workers which the queen has been the first to procure. Now the queen of *sanguinea* is very particular about the genus and the species of the ant whose colony she raids when founding her own. The typical European *sanguinea* ordinarily raids only the colonies of the typical *Formica fusca*, the common black pavement ant of Europe, which is of the type which includes our own common "black ants."

In this country, the queens of the various subspecies of *sanguinea* raid only colonies of ants of the *fusca* group, especially the subspecies *subsericea*, *subaenescens*, *subintegra*, or rarely of another species-group, the *pallide-fulva*. The workers, in general, are equally specific in their preferences, and raid for slaves only the species which was originally procured by their mother to found the colony. This is not invariably true, to be sure, for *sanguinea* retains the old habits of *rufa*, and

sometimes raids colonies of quite unrelated ants and pillages their larvæ. These, however, are devoured almost at once, and very few ever come to maturity in the colony. Usually only a small proportion of the captured *fusca* pupæ are devoured. The rest are carefully tended and reared. The greatest interest is taken in the captured brood by members of the slave species already present in the colony, and they are often predominantly active in caring for the closely-related newcomers.

The number of slaves which may be brought to maturity in a colony varies greatly with the subspecies of *sanguinea*. The typical European *sanguinea*, although it normally brings a large number of slave pupæ into the nest in the course of the summer, hatches but few of them. It would seem, in this species, that the primary hunger-instincts of *rufa* still predominate, since by far the greater number of the young are devoured before they become grown. Among certain of the American subspecies, no young whatever of the introduced species are brought to maturity, and the colony becomes pure with the death of the first alien brood reared by the young queen. However, the great majority of the American subspecies include large numbers of slaves within their colonies, the numbers of aliens present being sometimes greater than those of the enslaving species, and contributing not a little to the welfare of the group. Undoubtedly, these ants undertake more forays in the course of a season than does the European form, but not in proportion to the greater number of slaves present. This discrepancy in the slave-slaveholder ratio would seem to be accounted for best by the fact that a larger percentage of the captured

young are preserved to maturity than is the case with the European form.

Concomitant with this intentional preservation of alien young which distinguishes the customs of *sanguinea* from those of *rufa* has come a tremendous increase in the care given to the method of obtaining them. In contrast to the casual, disorganized robbery of *rufa*, the workers of *sanguinea* are very systematic in their pillaging activities. A large share, if not all, of the workers of a *sanguinea* colony leaves the nest in concert on the day of the raid, straggling along, typically, in a more or less broken column, but proceeding with remarkable directness to the site of the doomed community of the slave species. It is notable that there are no leaders of the column, but that any ant can function as guide. Here again, as in so many other activities of ants, there is a complete absence of any procedure of direction as it is understood among human communities. Having reached the predetermined site, the *sanguinea* column, after considerable hesitation, attacks the alien colony, enters it, and attempts to make off with larvæ and pupæ without, destroying adults unless resistance is offered. It has been noticed by many observers that the whole procedure is carried out as peacefully as is possible, so long as the raiding ants obtain all the available booty. Once the larvæ and pupæ have been secured, the column straggles home. The pupæ and larvæ are deposited within the home formicary, and are immediately taken over by the members of the slave species, which do not leave the colony on foray.

Several things are to be noticed about the relationship of *sanguinea* to its slaves. *Sanguinea* is by nature more favored than any of its slaves—indeed, it is believed

by many to be the most gifted of all insects. Consequently, the slaves are certainly no more competent to perform service in the colony than would be an equivalent number of the slave-making workers. The slaves are physically weaker, on the whole, and decidedly less competent. They are therefore functionally subordinate to their captors. Their activities are confined to nursing of the brood, and possibly to foraging for ordinary types of food, to attending aphids if any are present, and to a little excavating. All major colonial activities, however, are carried out by *sanguinea* without reference to its slaves. The slave-makers shift their nesting sites many times, often in response to a dearth of slave colonies in the vicinity. In addition, they regularly maintain summer and winter nests, and migrate from one to the other of them in the spring and fall. All of these movements are initiated and conducted entirely by the *sanguinea*, and the slaves are ordinarily actually carried from one nest to the other, exactly as though they were incompetent larvæ or pupæ. The architecture of the nest is characteristic of the slavemakers, and does not resemble that of the nests from which the slaves have been taken. In short, the slaves are to their mistresses much as a low order of unskilled labor is to a highly trained farm employer. They are aids in the expediting of work, but there is nothing which they can do which the slave-holders cannot and do not do themselves, while there is much in the lives of the slave-holders which is not comprehended by the slaves. The institution of slave-holding, so far, has been without gross influence upon the characteristics of the slave-holders, although minor effects have already made their appearance. The whole situation offers a rather close parallel to that of

the plantation owners and the black slaves of the old American South. As with the ants, the slaves here were not essential, except in a purely economic sense, and did nothing which their masters could not themselves do as well. On the other hand, all of the projects undertaken on the plantation were at the initiative of the slave-holder, and the characteristics of the group were those of Cavalier England rather than of Liberia. Furthermore, there was much in the life of the plantation owner which was not understood by the slave. There was little in the life of the slave that was not at least fairly familiar as a concept to the planter. However, as with *sanguinea*, minor modifying influences had undoubtedly been exercised upon the planter before the Civil War which rendered him at least more understanding and tolerant of the Negroes, and to a slight degree an imitator of their customs.

Except in very unusual instances, this is the furthest development to which mankind, in its social youth, has ever carried the institution of slave-keeping, and so we have no evidence, among ourselves, of the ultimate consequences which slave-holding may bring about in the life of the slave-holder. It is otherwise among the ants, for the *sanguinea* phase is but the second in a long series of stages of the art of enslaving alien races, which the ants have practiced much longer than have we.

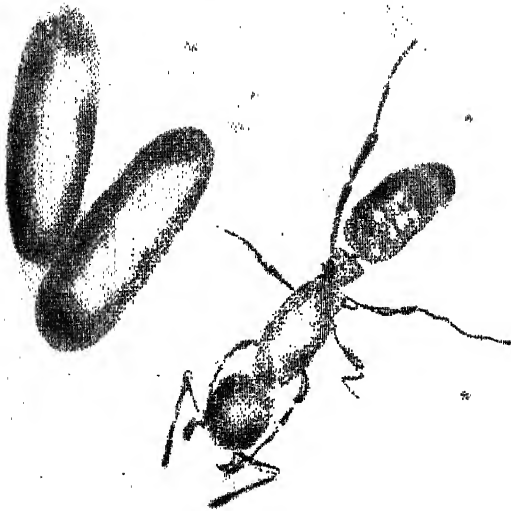
The third stage is represented by another Formicine genus of great brilliance, which, like *sanguinea*, occurs in Europe in a single species, and in America in several widely differing subspecies. The genus *Polyergus* is composed of ants which are without exception keepers of slaves. The slave has become an absolute necessity to the economy of the colony.

Ants of the species *Polyergus rufescens*, and its corresponding American subspecies *lucidus*, *breviceps* and *bicolor*, are large, handsome, red insects of great beauty, alertness, and activity. As with *Formica sanguinea*, the young queens habitually found their colonies by dispossessing incipient alien communities of their young, and the species used for the purpose are the identical ones employed by *sanguinea*, with which *Polyergus* geographically coincides. Similarly, the mature colonies raid communities of *Formica fusca*, *subsericea*, *subaenescens* and *subintegra*. One subspecies pillages only the *pallidifulva* group of *Formica*. There are several very important and significant differences between the two slave-holding types, however. *Polyergus* gives every evidence of being a far more experienced holder of slaves than its congener. The slave raids are carried out with greater precision and brilliance than those of *Formica*, and are military forays that are very wonderful to watch. They are performed without any hesitation. The entire column is pervaded, during the raid, with a powerful excitement, which is perhaps equaled elsewhere in the ant world only by the drivers when they are pillaging. The entire expedition is undertaken in concert, as though by word of command, and is carried through with a dispatch and definiteness of aim which almost compels one to believe in the existence of commands. The raid is completed within a remarkably short time. Once the column has returned to its own nest, however, and the stolen pupæ have been given to the eager slaves for rearing, the behavior of the late warriors changes completely, unlike *sanguinea*, and they loiter indolently about the formicary, paying no further attention to colonial duties. Slave forays are under-



A TYPICAL FORMICINE ANT

Formica fusca subsericea is the common "black ant" of our pavements and typical of the highest division of ants. It is the species enslaved by the facultative black-and-red slave-maker *Formica sanguinea*, and the type species is enslaved by *Polyergus*. It maintains many queens in a single community by the device of capturing young, freshly fertilized queens at flight-time and persuading them to abandon their usual methods of colony foundation and be adopted into a mature community instead. There were seven queens in this colony. (Schenectady, N.Y. *Original*.)



A PONERINE ANT AND HER YOUNG FIRST BROOD

The method of colony foundation of Ponerine ants is still uncertain. That it may well be that of "partial provisioning," however, is indicated by this isolated young queen. Taken as a solitary insect without young, she laid eggs and reared a brood without assistance. She is shown attending them. (Ituri Forest, Belgian Congo. *Photo by D. M. Gallagher.*

taken more frequently than is the case with *sanguinea*, and the percentage of the young captured from a given raided colony is probably higher, due to the greater efficiency of the captors. The proportion of pupæ devoured seems to be small. Consequently, as might be expected, the proportion of slaves to slave-holders in the *Polyergus* nest is far higher than with *sanguinea*. The ratio between slaves and slave-holders is in fact reversed.

The position of the slave in the *Polyergus* colony is a very different one from that in the *sanguinea* formicary, even though the slave species may be the same. The slave is compelled to assume the complete burden of conducting the domestic life of the colony. The slave-holder is a brilliant warrior—far more so than even the accomplished *sanguinea*—but in other matters its interests have lapsed completely. It has no concern whatever in the care or rearing of the brood, either of the slave species or of its own. The broods are raised entirely by the slaves. Similarly, the architecture of the nest is of no concern to its owner. All excavation is done by the slaves, and the form of the nest is that of the slave species. How truly has Spengler* said: "When a house type vanishes it means that race is extinguished." Not only is *Polyergus* little interested in its nesting site, but it is compelled to abandon it and to move about at frequent intervals, in literal pursuit of wild communities of the slave species, upon which it has now become completely dependent; for a number of structural specializations have taken place simultaneously with the high specialization of instinct in this military species. The mandibles, which in *sanguinea* are dentate, as among most non-slave-holding and self-sufficient

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species, and adapted to the transportation of young, of food, and of earth grains, to the excavation of the nest, and to the general conduct of colonial life, have in *Polyergus* lost all their tooting, and become, instead, smooth, polished, curved, sickle-like structures, with sharply pointed ends. They are completely useless for all ordinary purposes, but are beautifully adapted to piercing the crania of refractory members of the slave colonies, should these resist the deportation of their young. The mandibles are customarily used for this purpose by *Polyergus* in its forays. Recalcitrant defenders of the citadels of the slaves are grasped by the sickle mandibles, the points of which are held in apposition over the brain cavity. Usually the defender is carrying a larva or pupa when it is attacked. If the burden be promptly released, the nurse ant is set free unharmed. Otherwise, the points of the sickles meet through the brain, and the defender collapses.

Although this high specialization handicaps the ant to some extent for all more domestic activities, this modification alone is not too serious. The ant is not completely incapacitated for the caring of young by this modification, as is shown by the fact that it is able to bring home the young which it has secured on its expeditions without damaging them severely. However, a change of much graver significance has taken place in the mouth parts. The tongue has become so shortened that the ant is no longer able to take food without assistance, and must be fed by its slaves. Without their constant aid, the warriors of the slave-holders will perish of starvation in the midst of plenty, in their own colony. It is striking to observe a colony of *Polyergus* in the artificial nest when, for one reason or another,

the slaves have refused longer to attend to the personal wants of their mistresses. The mistresses rarely beg to be fed. Indeed, they appear to take very little interest in themselves or their surroundings, unless the prospect of a foray is in sight. If they are not artificially nourished, they die of starvation in the midst of plenteous food upon which the slaves are thriving. The warriors die as stolidly and indifferently as they have lived.

It is to be seen that the genus *Polyergus*, despite its apparent dominance and brilliance, has actually already turned the corner in this drama, and is no longer autonomous. All of its activities must now be governed by those of its slaves. Its habitat, the timing and the nature of its forays, the size of the brood it rears, the very abundance of its food supply, are all wholly dependent upon the number and the willingness of its slaves. Its queens can only establish their colonies under very special conditions, and in consequence, we find that, as a group, ants of the *Polyergus rufescens* type are far rarer insects in both the New and the Old Worlds than are those of the *sanguinea* family. The social position of the worker is faintly reminiscent of that of the human city dweller, whose work consists in increasing the perfection of a single phase of the life of that city, but who, through his specialization, has completely lost his independence, and has in fact become but a miserable parasite upon others of his kind. His position is still one accorded great respect in the large cities, and his position is higher the higher the degree of his specialization. Very few realize the fearful sacrifice which has been made and the helpless position which the "leader" actually occupies in any but his own particular environment. So it is with *Polyergus*, clothed

still in an exterior of military brilliance to hide the actual parasitic tendencies beneath, and able still, because of specialized strength and military genius, to hide the great price which has been paid for the surrendering of independence.

In the next stage of the story we see the disguising cloak beginning to fall away. The third and fourth chapters of the tale deal with Myrmicine, rather than Formicine ants. The story is therefore discontinuous at this point, since the Myrmicines can hardly have been derived from the Formicines. There is much evidence, however, to indicate that the next two groups to be considered were derived from ancestors essentially like *sanguinea* or *rufescens* in their slave-holding habits, and therefore represent the last stages of an evolution parallel to that represented by the two Formicine ants already discussed, a *dénouement* to which even the Formicine ants, let alone mankind, have not yet attained.

The Myrmicine genus *Strongylognathus* comprises a series of slave-making ants which is confined to western Siberia, Asia Minor, the shores of the Mediterranean, and to Europe, where its range somewhat closely coincides with that of *Polyergus*. Like *Polyergus*, again, it takes no interest in feeding, in the care of the young, or in the excavation of its nests, which are taken care of entirely by the host group. Its choice of slaves is much more restricted than that of *Polyergus*, only a single species being used, *Tetramorium caespitum*.

The mandibles of *Strongylognathus*, like those of *Polyergus*, are narrow, curved, and pointed, and admirably adapted to piercing the heads of refractory enemies. One important difference is manifest, however. Splendidly adapted as these mandibles are to pierc-

ing ant heads, their muscles have become so weakened that the insect is actually powerless to carry out the act! All real military authority of these creatures over the colonies which they raid is therefore gone. Nevertheless, the gesture is still faithfully retained in *Strongylognathus huberi*, and so slowly do ants learn that a bluff suffices to achieve the end in view! Members of the slave species, when attacked by the raiding columns of *Strongylognathus*, when their heads are taken into the opened mandibles of their assailants and pressure is applied in the cranial region, forthwith drop their larvæ or pupæ, totally unaware of the powerlessness of the raider to enforce its will. The discarded pupæ are gathered up and taken home; but forays upon colonies of *Tetramorium* are necessarily bloodless affairs, conducted upon empty threats as far as the mistresses are concerned.

There is one important difference between the slave raids of the Formicine ants which we have considered and those of *Strongylognathus huberi*. The latter in their expeditions are accompanied by their slaves, which actually do most of the fighting. So, at this stage, the sphere of activity of the slave has invaded even the region of military campaigning, formerly the one *raison d'être* of the slave-holder. The activities of the slave, or the host, as it may now properly be called, have come to dominate completely those of the slave-holder, now become parasite.

This development is carried still further in another species of the same genus, *Strongylognathus testaceus*. *Testaceus* has abandoned all attempts at slave raiding, in final functional recognition of its helplessness. Like its Formicine homologues, and its allied species, *huberi*,

the young queen of *testaceus* seeks to enter alien colonies of *T. cæspitum*. There is an important difference of procedure to be noticed between the Formicinè and Myrmicine queens, however. Whereas the young queens of *Formica* and *Polyergus* habitually slaughter the adults of the feeble colonies which they attack, and bring up the larvæ, so that their adopted allies are always younger than themselves, the queens of *Strongylognathus testaceus* seek by stealth to enter flourishing colonies of the host species, and to be accepted by and to remain in company with workers older than they. They thus approximate the position of true parasites, and remain throughout their lives in the one colony to which they have obtained entry, with no attempt at forays, which indeed have now become both undesirable and impossible, owing to the abundance of alien worker help at hand, and the extremely small proportion of the colony which is made up of the invading parasite. The host queen may be killed, so that only young of the parasite are present, but in the more degenerate colonies she is allowed to live, and the young of both species coincide in the nest.

Other parasitic features have become noticeable. The young parasitic queen, supplied from the very beginning with abundant food procured with no effort or expense to herself, begins to produce sexual forms, queens and males, at a very early age, and in great numbers. This development corresponds very closely to the tendency of parasitic organisms in general to produce great numbers of sex cells, thus overcoming to some extent the terrific hazards which the young will have in finding safe positions with the appropriate hosts. The worker caste, under these conditions, is entirely superfluous; and

in *Strongylognathus testaceus* it is markedly diminished in numbers.

The final stage is attained in a series of Myrmicine genera best represented at the less degenerate end by *Wheeleriella*, and at the more modified extreme by *Anergates*. The queens of both types seek adoption in their host colonies. Only a single host species is affected in either case. The queens, once within the colony, contrive to become amicably adopted by their hosts. They pay no attention to the host queen, but for reasons of trophic unbalance poorly understood today, she is almost invariably assassinated by her own workers very shortly after the adoption of the alien queen. Immediately the intruding queen proceeds to lay large quantities of eggs, which are cared for by the host workers. These develop immediately into young queens and males, the worker caste having been eliminated entirely. The young queens and males of *Wheeleriella* are more or less normal in structure and behavior, and escape from the host colony and undertake the marriage flight in the classical fashion, the aberrations of behavior becoming evident only at a later time. With *Anergates*, however, the male has become structurally degenerate, is wingless and undeveloped even at maturity, and quite unable to care for itself at all, or even to leave the nest. Mating therefore takes place within the host formicary, between brothers and sisters, after which the young females escape and seek colonies to enter. Once they have secured homes in them, their abdomens swell with the production of eggs so that they, too, soon become incapable of any great movement. The females of both of these genera can live only so long as the longest-lived workers of the host species, for, since the host queen is assassi-

nated, no new workers can be produced, and the queens are unable to care for themselves. The period of their lives is therefore drastically restricted, and it is of advantage to them and to the genus to produce the sexual forms immediately—forms which, in autonomous, self-supporting species are rarely produced within less than five years after the formation of a colony.

So at the end of this remarkable development, whose inception we see in the brilliant slave-making habits of the able *Formica sanguinea*, we find degenerate parasitic forms which have returned to the solitary, workerless condition of the ancient Vespoid ancestor of all ants, eking out an existence yet more precarious than that which was enjoyed by this generalized Tertiary earth-dwelling wasp. It is an existence, too, the more hopeless because it cannot possibly, it would seem, have any result other than the extinction of the entire unfortunate race. Already the genera of workerless ants are excessively rare, and seem to be facing universal extinction in the near geological future. Such is the ultimate issue of the custom of slave-making!

There are many interesting and significant features to be noted in this whole social evolution. One of the most striking is the subtly increasing influence which seems to be exercised by the slave upon the slave-maker as the institution of the slave-making comes to be more perfect and as increasing reliance comes to be placed upon it by the mistress species. We have seen that the influence of the *subsericea* slaves upon their *sanguinea* mistresses is subtle, but probably no more profound than that of the negro slaves upon the white society of our South. The condition becomes much more marked with *Polyergus*. However the situation may have arisen,

it is a fact that the various subspecies of *Polyergus* differ from one another in temperament and structure in a way markedly parallel to that in which their slave species differ among themselves. Thus *Polyergus rufescens*, and its subspecies *bicolor* and *breviceps*, which habitually enslave ants of the *Formica fusca* group, resemble that ant in their rather aggressive temperament, in the possession of large colonies, and especially structurally in their thick-set, compact build, rather dull coloring, and the great development of hair upon the body. *Polyergus lucidus*, on the other hand, enslaves ants almost exclusively of the *Formica pallide-fulva* group. These are extremely quick and nervous in movement, and timid in temperament. They form small communities. Structurally, they are rather large individuals, very smooth and shining and of a loose, "gangling" body type, with very long limbs and antennæ. The *lucidus* resemble them in every particular, being large, gangling, long-limbed ants, with beautiful shining armor of a brilliant red. They are timid and retiring by nature, and form small, scattered communities, almost exactly like those of the slaves. The resemblance of host to slave is carried much further in *Strongylognathus*, which resembles its *Tetramorium* host very closely, both in size and in coloration.

The effect of the host upon the slave species is less evident and more subtle, perhaps, because, with the exception of that of *sanguinea*, the slave has little to gain by imitation. Nevertheless, indubitable effects are to be found, most particularly upon the temperament of the slave. *Formica subsericea* is normally a timid species, but workers held as slaves in large and aggressive colonies of *Formica sanguinea* come to be pugnacious, and

will defend their adopted community with much aggressiveness when it is threatened. The writer has seen the *pallide-fulva* slaves of colonies of *Polyergus lucidus* kept in artificial glass nests practicing upon one another, during idle hours, a crude imitation of the tactics of attack and deportation which are used by the hosts in their forays. This condition seems to have gone much further among the *Tetramorium* slaves of *Strongylognathus huberi*. These have actually adopted the complete slave-making technique of their hosts, and have been induced to make predatory raids upon the neighboring colonies of their own species, with the sole purpose of obtaining additional slaves, as we have seen. They are in fact the effective portion of the raiding columns, for the slave-makers are structurally incapable of dealing with the raided species. The slave-holders, in this case, appear to be present in the column merely as spectators, and function, in anthropomorphic terminology, only as moral supporters. This raiding habit is entirely foreign to the workers of normal colonies of *Tetramorium*. The manner in which it is acquired by those individuals whose learning period is spent with *Strongylognathus* is unknown. Its discovery could not but throw the most interesting light upon many difficult problems of ant learning in general. Finally, we cannot overlook the extraordinary influence of the purely parasitic queens of the workerless species of ants in inducing, apparently involuntarily, the assassination of the host queen by her own workers—a move highly coöperative from the standpoint of the parasite, and racially suicidal from the viewpoint of the host. It is relatively easy to understand the adoption of an alien queen into a colony on a purely trophallactic basis, by a

perversion of the trophallactic instincts, such as will be described in another chapter for the case of true parasites. But it is difficult to see how an alien, intruding individual in a huge host colony could contrive, while paying no attention whatever to the host queen, to render that individual so distasteful to her own workers as to lead to speedy assassination. Such situations remind us anew of the tremendous depths of mystery which still surround the operation of that wonderfully delicately adjusted mechanism which is a colony of the commonest ants.

In the institution of slave-making among ants, with its ultimate end in abject social parasitism, we have an excellent example of the sort of social prediction which a study of the Formicidæ can make possible in terms of human affairs. The situation of *Formica sanguinea* we have paralleled in our own experience. The institution of slave-keeping among humans has in general been terminated at the point of evolution of *sanguinea*, because economic factors to which ants are not subjected have intervened. In general, therefore, we cannot follow the parallel further. Yet, in a few isolated instances among older human civilizations, we can glimpse a local approach to the *Polyergus* and even to the *Strongylognathus* stage. Witness the social position of more gifted slaves, and especially of the royal concubines and the eunuchs of the courts among the ancient Chinese and Manchu civilizations. Within the restricted bit of the social structure represented by the royal entourage, where hypertrophy of social development reached its furthest extreme, a relation between slave-holder and slave developed which approached that of *Strongylognathus* and *Tetramorium* very closely, wherein the slave

was dominant, in all but name and position, and took the lead in most of the affairs of state. The same condition in much milder form was to be found in the Paris of the later Capetian monarchs—milder because the social system so developed was at once much less isolated and perished at a much younger stage than was the case in China.

There is every evidence that, given sufficient economic advantage, sufficient isolation, and sufficient time in which to develop, the institution of slave-keeping in the human race would follow a course closely parallel to that of the ants, and would terminate in a miserable condition that we of the present can hardly visualize and much less would wish to—the complete social decadence of a once vigorous race of mankind. Happily, man's greater physical bulk, his keener awareness of his own kind, and his far more complete conquest of space by reason of the mechanical age which he has exploited so fully, represent advantages in his struggle against this sort of social decay which are absolutely inaccessible to the ants. Such unique advantages should prove most effective through the coming years in preventing this, one of the most revolting imaginable types of social disintegration.

The Tributary Peoples

THE INSTITUTION OF SLAVERY represents one of the most striking aberrations in the social lives of ants. We have seen in the preceding chapter how deep and far-reaching the effects of this institution may be upon both slave and slave-holder. The parallel in human society, as we have seen, extends only to *Formica sanguinea*. Beyond that point human society has not had time to go, but one can gain some inkling of what might happen were it to persist consistently over many thousands of years. We now turn to another situation in ant society which is of not infrequent occurrence and which probably tends to the same end as slavery, and in which the parallel among human societies can be extended somewhat farther.

Frequently colonies of two entirely different and independent species of ants will nest in very close proximity to one another, and will use nest entrances which are but a short distance apart. The colonies are often hostile, and were drawn together originally by no interest whatever in one another, but purely by some par-

ticularly attractive, local feature of the environment, such as a warm stone. It is almost necessary, in the first, most primitive condition of this association, that the two species be very different in habit, and that they be composed, respectively, of very large or very small ants or of a very timid and a very bold species. If such differences did not obtain, life would hardly be tolerable between two aggressive groups whose own ideas of a suitable habitat were so similar, and the colonies would necessarily either become friendly and fuse, or one would drive the other out.

It is evident that the former course, that of at least temporary fusion, must sometimes take place, for occasionally we do find two colonies of ants of species of similar stature and habits nesting in close association. The files of workers leaving the nest may be composite, each species being represented. The two groups may proceed together to a common feeding ground, but then the file will divide, and each colony, thereafter, will continue independently in its task of gathering food. The two colonies will rigidly respect the integrity of each others' nests, and their broods will be brought up independently. Such an association seems a harmless one to the social lives of both parties, yet it contains the germ of trouble when it is carried to an extreme. Already a very great concession has been made, for, as we have seen, normal, adult, independent, and healthy colonies of nearly all ants are vigorously hostile even to foreign members of the same species.

The next step in the relationship is represented today by a number of pairs of associated species of ants in which a quite definite tributary relationship has been set up, which is in many respects not too unlike the trib-

utary relationships occasionally seen in the history of feudal human society, both Occidental and Oriental. One of the most interesting of such pairs comprises the boreal species *Leptothorax emersoni*, a rare ant known only in the New England States and probably eastern Canada, and *Myrmica canadensis*, a common Myrmicine ant of the northern half of the United States.

Myrmica canadensis builds its formicary by choice in moist, soft, peaty earth, preferably in the soil of bogs and adjoining decaying logs, or under deeply buried stones, where it runs its galleries for considerable distances between earth and rock. It is a wholly independent species, with large queens, and is in every colonial respect the most normal of ants. Rarely, however, a colony of *Myrmica* is to be found in association with the relatively tiny *Leptothorax emersoni*. The chambers and galleries of *Leptothorax*, far too small to be entered by a *Myrmica* worker, are placed extremely close to the formicary of the larger ants, but are maintained intact, with separate nurseries and brood-rearing chambers. They communicate with the *Myrmica* colony, however, by numerous small openings, and the little workers enter the *Myrmica* nest at pleasure, and wander about at will. Far from being hostile to these little neighbors, the *Myrmicas* welcome them with a sort of tolerant indifference, treating them much as dogs are treated by people who do not quite like dogs. The *Leptothorax*, on the other hand, are more than attentive to the *Myrmica*. They mount and ride them, lick them effusively and continuously in trembling excitement, and constantly beg food from the lips of their enforced hosts. The *Myrmicas* tolerate and sometimes even appear to relish this treatment, and feed their little masseurs so frequently that

the smaller species has come to depend upon this food supply, and does not seek any independent nourishment. Instead, it spends its whole time cleaning its hosts and soliciting meals from them. It is very careful, however, not to tamper with the *Myrmica* brood in any way, nor to commit any socially vicious acts which might upset the balance of the host colony. It is equally anxious that its own colonial privacy shall be respected, and never, under ordinary conditions, allows its own young to be mixed with those of the *Myrmicas*. Occasionally the *Myrmicas* themselves attempt to bring about such a mixture, break into the galleries of the *Leptothorax*, and seek to carry them back to their own formicary. The small ants immediately become hostile, seize the intruders, and do their comical, tiny best to force the *Myrmicas* to withdraw—an effort, curiously enough, which is usually successful. Under the conditions of the artificial nest, however, it is less often so, especially when earth is wanting in the nest and there is no convenient substance which the *Leptothorax* can build about their brood by way of a protecting rampart. In such case, a long and wearying struggle ensues, in which the *Leptothorax* larvæ are kidnapped by the *Myrmicas*, without, however, being damaged in the least, and are rescued by their own nurses. Ultimately, the nurses give up the struggle, and allow the broods to become mingled—a situation which they would never permit in the wild.

Leptothorax colonies apparently never normally nest apart from their large companions, and if isolated from them in captivity they display considerable dismay. They have partly forgotten the art of feeding independently, so long have they begged food from the *Myrmicas*,

but they are not dependent upon them for anything but food. When isolated, they gradually relearn the trick of independent feeding and food-gathering, at first rather awkwardly, but eventually quite like ordinary self-dependent ants. Thereafter their colonial life becomes as completely self-supporting as that of their autonomous cousins *Leptothorax longispinosus* and *Leptothorax curvispinosus*.

A relationship of this kind is of the mildest character. It would seem, if anything, to be beneficial, and of no possible harm to either partner. The *Myrmica* colony leads a normal life, produces numerous queens and males in standard fashion, and its members seem to derive as much benefit and pleasure from their association as benevolent St. Bernard dogs, surrounded by crowds of energetic and playful dachshunds. But any sort of dependence is bought very dearly among ants, as among men. We can see no harmful consequences of the association, as yet, for the hosts. Such consequences are becoming evident in the parasite, however. The loss of independent feeding habits, to be sure, is of relatively small consequence with *Leptothorax*, and they are easily relearned. But a physiological change of some moment has already set in. Spending their complete existence in comparative security, amid an abundant and constant food supply easily gained, these ants are freed from one of the main restrictions of the hunger society which we have earlier considered. No longer need the worker be in a constant state of semi-starvation, nor the small worker larva constantly underfed. The consequence is evident with *Leptothorax*, for the worker caste is already beginning to be lost by the gradual transition of its members into queen-like organisms. A large number

of the workers possess three simple eyes in addition to the two compound ones, a usual characteristic of queens. They possess queen-like thoraces, resemble the queen in stature, and have well-developed ovaries. They are almost permanently fertile, normally egg-laying, ergatoid females, whose function is that of reproduction rather than labor. *Leptothorax* is well on its way to losing its worker caste, and becoming completely parasitic, represented only by males and reverted queen-workers. The true queen is rare now with *Leptothorax*, and may be on the way to disappearing. Nowhere is there clearer evidence of the delicacy of the adjustment between queen and worker, or the ease with which it may be upset by relatively small changes in the social lives of ants.

A number of other ants are known which have taken up habits rather similar to those of *Leptothorax*, and in all of them the same sorts of aberrations are becoming evident among the personnel of the parasitic species. Particularly interesting among these are the species *Symmyrmica chamberlini*, of America, and *Formicoxenus nitidulus*, of Europe. *Symmyrmica* lives with the much larger *Myrmica mutica*, almost exactly as does *Leptothorax* with its *Myrmica* host. As with *Leptothorax*, the workers have come to possess three simple eyes, and to take on other queen-like features. The effect on the inquiline has gone further here, however, for the male has lost its wings, and begun to assume the appearance, although not apparently the function, of a worker—a development of great interest in view of the extreme social conservatism exhibited by the males of nearly all normal ants. Despite his winglessness and the worker characteristics which he has, however, the male is still readily recognizable as such by his rounded head, large

eyes, and enlarged thorax. With *Formicoxenus nitidulus*, the same subtle development has been carried much further. Not only is the male *Formicoxenus* wingless, but he has become so worker-like in structure and appearance as to be distinguishable from the worker caste only by very specialized features, and on rather close examination. Needless to say, the mating flight has been eliminated among these forms, and fertilization takes place on the dome of the parent formicary. *Formicoxenus*, itself a Myrmicine ant like *Symmyrmica* and *Leptothorax*, differs from them in that it selects a Formicine host. In all probability, this choice of host is a recent one, representing a transfer from some Myrmicine host, and indicating, as does the structure of the males, the more advanced and probably more ancient condition of the relations among *Formicoxenus* than with its American cousin. Such disparity is often observed in many features of the colonial lives of various pairs of closely related ants living in the New and Old Worlds. In many cases, the Old World ants present a more stable, more anciently fixed character than those of the New. This is the case with the slave-making habit among the European and American *Formica sanguinea*, as has been seen.

This loose intercolonial relationship of *Leptothorax*, *Symmyrmica*, *Formicoxenus*, and their allies would seem to be of the most noncommittal and harmless character. Parallels are not rare in human society. One of the most striking may be seen among those academic groups of scholars whose support must flow entirely, and often abundantly, from the public purse, and who, from the very nature of their occupation, can make no monetary return to that purse. Academic bodies en-

gaged in pure research, whether of scientific, literary, or canonical character, fall very directly into this class. They are essentially parasitic groups subsisting upon the provender of the greater society about them. Under proper circumstances, however, they are beneficial to their hosts, for their members have become highly specialized to perform tasks that are to the benefit of both societies, and which the working members of the host society, like the workers of the host colony, are not sufficiently specialized to undertake. Under proper circumstances, too, the work of the academic parasitic body is as arduous as that of the host—in very many cases much more so. The excess of economic “nourishment” with which it is supplied then becomes no more than that necessary to sustain a conservative, effective working body. In the event, however, that the work of such groups becomes sufficiently formalized and routine in character, or lacks sufficient arduousness completely to metabolize, so to speak, this more readily gained economic “nourishment,” a condition very closely paralleling that of the temporary social parasites of the ants may arise. The effect among humans, as among the ants, is felt by the inquiline long before it affects the host. This is a real danger that certain groups of men have faced in all ages. We need but to look at the mental perversion among the members of various religious and academic castes throughout the ages, after those castes had lived through and served the primary purposes for which they came into being, to realize this. Rarely has society as a whole suffered from the hypertrophy of such social groups, but the members of the groups themselves have often done so. This danger is as real today as it ever has been, and is one against which the members of some

of the most sensitive and helpful of our intrasocial groupings of today—which, because of their very high specialization, may be outmoded tomorrow—must ever be on guard.

The host species of ant in the type of inquilinism which we have considered is much less subject to effects from the relationship than the tributary people. However, the tributary people may become aggressive, exactly as in human society, and in such case the effects of the relationship become much more serious. The ants which we have considered at most obtain their food from the mouths of the members of the colonies with which they associate. The brood is never menaced by the little intruders, nor is any relationship essential to the balance of the colony disturbed. The opportunities to steal the brood, however, must at times be rather good, and it is hardly surprising that in another group of ants we find the tributary peoples themselves exacting tribute. Conspicuous among such marauders are the Myrmicine genera *Solenopsis* and *Carebara*, members of which range from the Americas to Central Africa. We have already mentioned in earlier chapters the "thief" ants *Carebara vidua* and *Solenopsis molesta*. The latter, an American species, is remarkably versatile. It may live in the dwellings of men, or independently in the fields, but it prefers to run its narrow, threadlike galleries between the walls of the colonies of larger ants, communicating with the chambers of the host ant by tiny openings. *Carebara* pursues the same tactics in the giant termite mounds characteristic of parts of Africa. All the members of this group show a great disparity in size between the queens and the workers.

The workers are nearly always monomorphic, the caste system being absent. It was apparently once present, and was subsequently discarded, as we infer from the immense discrepancy in size between the queens and their small workers—a size difference which presumably was once bridged by a connecting series such as we find today among the fungus-growing ants and various other tribes.

The profession of all members of this group is primarily that of thieves. The tiny, usually light-colored workers repeatedly enter the formicaries of their hosts, now with the purpose of openly pillaging the young rather than of merely soliciting food from the mouths of nurses. The tributary peoples have openly become bandits, and at this point the effect on the host colony as well as on the parasites becomes marked. The parasites, in fact, show the effect somewhat less profoundly than those of the preceding group, for they have declared open, if subtle, warfare on the occupants of the nests which they have invaded, and ask no quarter or special consideration. Their huge queens are indicative of the abundance of their food supply and of the easy access which they have to it. But there is a discipline to prevent the workers from acquiring many of the degenerative features which we have already noticed—for they must earn their keep continuously, and at considerable peril, by the theft of larvæ from their hosts, if the colony is to survive. And this theft requires much independence of action, and a stealth for which small size is eminently desirable. They have thus become, on a very large scale, equivalent to the more highly organized bandit and gangster groups of human society, whose members are often men of marked independence and

even of talent, and certain of whose characteristics, which fit most of us for the ordinary law-abiding occupations, are unusually sharply developed in consequence of the dangerous nature of their lives and the necessity for quick decision which is constantly with them. Such colonies are "outside the law" of both men and ants, and are competitive with these highly organized societies. Competition of this sort is a very hard taskmaster, for the advantage is all on the side of the organized society. The outlaw group is very different from the tolerated group which exists within a society by its sanction, lives at ease, and is protected from competition with it. The bandits live a more virile sort of life. And while it is one which is destructive to the hosts in a material way, there is little that is really insidious about it. The host queen is left intact, the adult workers are unmenaced, and the whole pattern of colonial life progresses as usual, disturbed only by the unnoticed loss, from time to time, of groups of helpless but unmourned younger members.

A sort of exploitation that is more dangerous because infinitely more far-reaching and much more difficult to combat, has its beginnings in the groups of ants considered earlier. So long as the *Leptothorax*, *Symmyrmica*, and *Formicoxenus* are merely tolerated and, while being careful to do no permanent damage, are fed and lavished with care, the injurious effects of the relationship will accrue very largely to the little intruders. But they are in a position to do great damage to the colony and to exploit to the very fullest their peculiar position, if they transfer their parasitic activities to some more essential feature of its life.

We have already seen a bit of the lives of the socially parasitic beetles in another chapter and shall mention

them again. There is a whole group of ants that apparently developed from the relatively harmless guests which we have already considered, which employ quite similar tactics to achieve the same ends. Members of this group are recruited from both the Formicine and Myrmicine subfamilies, but the latter, more ancient group is, as we should expect, the more abundantly represented. Especially interesting is the species *Formica difficilis*, and a variety of it called *consocians*. The queens of these *Formicæ* are minute, actually being somewhat smaller than the largest of their workers in size, and are wholly unable to found colonies alone—quite as incapable in this regard as the queens of their slave-making cousin *Formica sanguinea*, and very much inferior to them in physique. They make no attempt, as the young *sanguinea* queens do, to take a brood of young workers of an incipient colony from their mother queen and older worker-sisters by force. Instead, they are extremely conciliatory in their behavior.

The young female of *Formica consocians*, after descending from her mating flight, seeks refuge in a small community of the alien *Formica incerta*. Once within the nest, she hastily conceals herself among the brood, and so escapes detection for a time. Somewhat later, when both she and the host colony have grown used to the new condition, she proceeds to adopt almost exactly the same tactics as the beetles *Lomechusa* and *Atemeles*, which have already been mentioned, in exploiting the instincts of the hosts. The workers of *Formica incerta* are somewhat larger than those of *F. consocians*, and about equal in size to, or slightly larger than, the queens of the parasitic species. The parasitic queen exhibits a remarkable mimicry of the host workers, both in appear-

ance and behavior. She fawns upon them as the beetles do, solicits food from them in the same way, and in addition, sometimes actually feeds them. There is much to indicate, moreover, that she develops a neutral or a pleasing contact-odor for the host colony, which ultimately causes them to lick and to fondle her as they do the beetle parasites. Soon thereafter, the young queen proceeds to lay her first eggs, and they are received and cared for like the eggs of the beetle parasites. The developing larvæ do not have the disadvantage of the beetles, however, that they require a different sort of care from the ant young, and large numbers of them successfully reach maturity. These young *consocians* workers gradually take over the functions of the colony, and a mixed group is formed. The *consocians* queen pays no attention to that of the *incertus*, but it is a fact that the latter soon disappears, though how we do not know at present. Gradually, then, the old *incerta* workers die off, and the young *consocians* colony takes its place as a pure, independent, and aggressive organization, with no hint whatever of its dubious origin.

The tactics of the young queens of *consocians* are somewhat like those of the beetle social parasites. In another related ant, *Formica ciliata*, the queen actually bears the same tufts of long, fragrant hairs which prove such a fatally fascinating attraction in the case of the beetles. Species of two or three genera of Myrmicine ants carry out similar practices. Finally, with the *Bothriomyrmex*, whose young, intruding queen eventually decapitates the host queen and thus eliminates her, we come to the peak of development of this socially parasitic line, which merges insensibly to that of the ants without workers, which we have al-

ready considered in connection with slavery. In all probability, the striking members of the workerless ants have been recruited partly from the slave-making types, which drifted into colonial parasitism through a method that was at first forceful and aggressive in character, and partly from a group which has been stealthy, passive, conciliatory, and sinister from the beginning, and bears a close resemblance to the beetle parasites of ant societies.

The effect of the lives of these creatures as a species on their hosts as a group is still not too severe, except in the colonies which are actually infested. The host species undergoes no adaptation to the relationship whatever, and, since the parasite almost invariably selects for its host a species of ant which is at once cowardly—and therefore readily approachable—and prolific—and therefore readily available—the host species suffers relatively little from the depredations of the parasite, unless the parasite is over-abundant. The parasite workers, moreover, do not suffer as much modification, actually, as do those of the *Leptothorax* type, for, after the first generation of the host workers dies away, they are compelled to fend for themselves in completely independent fashion, and they must remain fit for the task. The whole parasitic habit, however, is epitomized in the queen. The minute stature, the special hairs, the brilliant color, the polished and aberrant armor, all reflect the way of the life of a social parasite, and the modifications which that way of life demands. The distribution of the parasites is in general limited and somewhat erratic. For the most part they are rather rare ants whose range, while generally coinciding with that of the host species, is much less regularly filled. It is evidently no simple task for these young, impoverished parasitic

queens to gain entry to the host colonies; the failures must be very frequent. But once they have accomplished the task, their success is almost assured, and a flourishing colony develops. But how many must perish for each fortunate individual that succeeds!

The type of social parasite which, beginning as a small group at first merely tolerated within a larger society, eventually gains much favor in the group and is finally adopted and completely replaces the earlier social form, finds a striking analogue in human society in some of the transitions of religious and governmental institutions with which history is replete. The introduction of Buddhism among the people of Inner Mongolia by the Chinese, undertaken primarily as a step in the pacification of that warlike race, is an example of this sort. Introduced into a warlike nation by the pilgrims and priests of a more developed and cultured but pacific and physically inferior society, it gradually gained acceptance and finally adoption and devotion, and soon transformed the habits, customs, and character of a whole people, quite without bloodshed, or, indeed, without any form of physical resistance. Much missionary effort in many religions among peoples not of those religions falls into the same category, especially when the new worship is enthusiastically accepted and profoundly modifies the habits and cultures of the host people. Exactly the same sort of transition can be observed in a change of governmental forms, and is eminently characteristic of every important bloodless revolution in history.

If the analogy to the case of *Formica consocians* and *ciliata* is to be perfect, the new mores must completely replace the old. Many other situations that arise in human society resemble more closely the case of the

workerless parasites, where the intruding social structure develops within the parent culture and is nourished by it without immediately destroying it. The history of Egypt, Greece, and Rome is filled with examples of such conditions, arising mostly in the latest, most opulent, but often least resistant stage of the civilization. Such are the rapidly shifting religious sects, each highly specialized in its own right and demanding much of the social groups which supported it and of civilization at large, which characterized each of these three cultures toward its close, and of the political excesses of the same periods, with their consequent heavy levies of taxation to support an ever-increasing bureaucracy of essentially parasitic citizens. As with the parasitic beetles, these individuals multiplied in those societies with enormous rapidity, though by acquisition from the ranks of the non-political, who saw an easy means of existence offered, rather than by actual descent. Ultimately, as with the beetles, the weight of the accumulated parasites became too much for the body politic, and it sank, overwhelmed by younger, more vigorous, and more social-parasite-free societies. Every human nation, as it ages and its social margin of reserve increases, tends to accumulate these parasitic individuals and organizations from among its own members—groups which frankly exploit it, depending upon the margin to carry them in safety. And in every case the margin does support them, backed up by a normal and hard-working citizenry of unrecognized patriots, sometimes for centuries. But finally too much is expected of it; it is overburdened with non-productive commensals, and the whole structure crashes to the ground, carrying to death alike the remaining

normal citizenry and the parasites who have brought about the destruction. And as the original infestations of *Lomechusa* and *Atemeles* in the colonies of *Formica sanguinea* result in the production of aberrant adults, the pseudogynes, from normal larvæ—adults which are themselves parasitic, useless burdens on their colonies—so does a small nucleus of a vicious political, moral, or social influence in any society attract to itself numbers of indifferent youthful members of the society, and actually mold them into effective parasites upon it. As with the parasitic ants and beetles, the individuals of the vicious sub-societies, if long tolerated and cultivated by their hosts, eventually become as helpless and effete as the nobility of the late Roman Empire—so highly specialized to their peculiar situation that, in the event of any sudden change in it, they are worse than useless, and perish rapidly.

In war, in slavery, and in their tributary peoples and racketeers, ants exhibit an undoubted parallelism to the corresponding phases of human society—a parallelism that is the more instructive in its finer details in virtue of the immense antiquity and the exquisitely fine development of ant society as a whole. In conclusion, we turn to one more phase of the social relationships of ants which bears a striking resemblance to the corresponding relationship in human society. It is the treatment which the ants of highly advanced civilizations have accorded their less gifted and fortunate neighbors, and the corresponding attitude which these neighbors have, on their part, taken toward the aggressors which have continually robbed them of their best nesting and feeding grounds. We turn to a short consideration of

the relationships which exist today, in general, between the primitive ants of the Ponerine subfamily, on the one hand, and those more socially developed members of the Dolichoderines, the Myrmicines, and the Formicines, on the other.

The Fate of the Primitives

THROUGHOUT HISTORY, primitive man has been most shabbily treated by his more advanced cousins whenever they have competed for anything which they really heartily desired. More ancient man killed, pillaged, and stole wherever he could, without any attempt to spare his less competent neighbor when competition arose. There was little mercy in early Europe during the Celtic invasions which brought such ruin to Neanderthal and even to Cro-Magnon man, and but little more when the Celts in turn, with their differentiated tribes, were displaced by the Roman legions. The Egyptians seem to have made no concessions whatever in their relentless drive which pushed barbaric races to the darker parts of Africa below the Nile basin, and we must imagine similar relentless pushes by the early colonial Japanese against the Ainu, by the Norsemen at Lindisfarne, by the Spaniards in Latin America, and a thousand other instances. The primitive population was never wholly exterminated, but it was largely displaced and forced to seek less desirable dwelling ground, to which it usually

became passionately devoted in time. It is possible that Neanderthal man survived in Europe for a relatively long time in the deeper fastnesses, as we know that the Carib Indians did in the interiors of some of the West Indian Islands, and the Mexican Indians in the center of their country. Primitive and more advanced aggressor peoples sometimes subsist side by side for long periods, provided the vanquished race takes care to demand only the leavings in hunting grounds or food or locations for its homes.

Modern man, despite his pride in his greater enlightenment in dealing with vanquished peoples, proceeds in much the same fashion. At times much consideration has been shown the American Indian, the Polynesian and Melanesian peoples, and the natives of Australia. Especially in the last case, the treatment has been consistently thoughtful and, it seems to the conquering people, beneficial to the subject race. But always the same thing occurs. The conquered race diminishes in numbers; its fragments drift to stonier grounds. It spends the rest of its independent existence amid barren surroundings not touched by the conquerors, finding in its adaptability to hard living conditions the only sanctuary which enables it to continue a bearable self-dependent life at all.

The consistent results following the contact of socially developed peoples with more primitive ones have their counterpart among ants. Ants are well suited to give us an answer in this connection owing to the relative solidarity of the Ponerine subfamily as a whole, the extent to which it is set apart structurally, mentally, and socially from the higher ants, and the fact that it seems to have been a dominant, homogeneous worldwide fauna

in times when the recent ants had not yet evolved. Conditions have changed widely for it in the latter millennia, but it has been by no means affected to the same degree over all portions of its formerly world-wide range. In Australia, as we know, it has been completely protected in its ancient dominant state until quite recent times. The same, on the whole, has been true in the deeper jungles of the Old and New World tropics. In more barren, drier tropical regions, however, where Mesozoic conditions have more radically altered, and in the temperate zones, where they have undergone the shock of glaciation and subsequent competition with recent, prolific, and pugnacious types, the primitives have had quite other conditions with which to deal, and their course of life there has been far different. So today we can see the complete series representing the changes in these primitive creatures, from the time that they were the undisputed mistresses of their realm, to the condition when modern competition has become altogether too heavy for them, and they have completely vanished as a culture.

Australia is preeminently the home of the Ponerines of today. There they are dominant among ants, both in numbers and in species, and their position is analogous to that occupied by the Marsupials among mammals before the coming of modern domestic animals to the ancient country. Ponerines exist in Australia in many varieties. They are for the most part aggressive, living in open, sunny spots, and building conspicuous formicaries. Ants of the primitive genus *Mymecia*, thought to include the most ancient Formicids, are mostly large eyed and athletic, and huge in size for ants. They sting fiercely and without reticence. They are more than a match for

most marauding animals, and do not hesitate to attack them on the least provocation. Their whole attitude is that of organisms which have been completely dominant for uncounted centuries, expecting to continue that dominance indefinitely—which, in fact, wild and untamed, do not know the meaning of failure or subjection. The influence of such forms as these has been felt by other Australian Ponerines; some of the types are decidedly smaller and of less positive habit, but in the main the pattern is that of a highly active, competent, aggressive, extraverted race.

Much the same condition is found in the American and Asiatic tropics, with certain modifications, however. Here also the Ponerines are extremely numerous, but they exist side by side with more prolific and advanced types, which compete with them strenuously for desirable living conditions. The Ponerines are handicapped in this struggle by their limited choice of nesting sites, since they have never learned to colonize anywhere but in earth or decayed wood, and by their limited selection of a food supply. Hence we find many more types which live quietly, relatively free of the livelier competition about them. Ponerines in the jungles live in damp soil beneath the heaviest rocks, in decayed logs, in the cracks and crannies of a thousand isolated boulders and drifted debris. Here they form small and unaggressive colonies. Such communities have no need for aggression, for they find suitable food in the myriad larvæ which inhabit the rotten wood, or in the nests of the neighboring helpless termites. These food sources are not so often exploited by the higher ants, and so a large measure of competition is avoided.

The tropical forests are filled with practically un-

known species of Ponerines, living isolated lives in their little communities, and sometimes enclosed forever from the sun. But the large, dominant types are here too, inhabiting open patches of ground, as aggressive and successful as ever. So abundant is the generous nurture of the tropical jungles that, despite the recent invasion of advanced ants, the old settlers still remain. Encouraged by an environment which has probably been extremely stable since their inception, intrenched in ground which they were the first to occupy, using hunting grounds not completely appropriated by the usurpers, these autochthonous creatures have held their own. There is a touch of reticence and caution in their behavior, however, which is not to be found in Australia, where the actual advent of any considerable numbers of modern types must be a comparatively new thing.

Reticence and caution in Ponerines become increasingly evident as we leave the dense tropical forests. On the more open tropical oceanic islands the numbers of species of Ponerines is greatly reduced, and, where they have met active competition with the modern ants, their habits of life have been completely altered. No longer do they build at all in open or conspicuous spots, but inhabit exclusively the dark channels of the earth. Many of them have become specialized as blind or amblyopic pygmies, victims of an inescapable cycle of civilizations. The genus *Odontomachus*, which includes some of the most modern, progressive, and aggressive of the Ponerine species, has fared conspicuously better in this connection. Swift-moving, relatively catholic in its taste for nesting sites and for food, it is in many respects much more like one of the higher ants than like the family to which it properly belongs. Accordingly, it has survived remark-

ably well in competition with later types in all of the Tropical portions of the globe, and is circumequatorial in its distribution. It has even pushed as far north as Bermuda on the Atlantic coast, though it is now fast disappearing, as we have seen, in competition with the ship-ant *Pheidole*, which besets it.

Ponerines, adjusted as they were to a relatively warm climate, suffered very severely during the glacial epochs, as much from their limited mobility as from their inability to endure cold. Throughout the northern portions of the New and Old Worlds they were exterminated or driven southward, and they have had the greatest difficulty in returning. Thus it is in these regions, today, that the fate of the primitives can most readily be seen. In the eastern United States north of southern New York State, but two types of Ponerines successfully survive. In Canada and in England and Scotland, there is only one species. These ants are small and slow-moving, and confined, for the most part, to tiny, simple, earthen nests. One of these types, represented by the ant *Stigmatomma pallipes*, is practically a purely subterranean creature, as we have seen. It is timid and extremely hesitant in demeanor, and its every move advertises fear and uncertainty. The eyes of the workers are nearly vestigial, and only the queens and males sojourn in the open air for a brief period in the late summer. Ants of the genus *Ponera* are not quite so conservative, for one can occasionally see workers emerging timidly and sporadically into the open air on damp days, remaining and foraging above ground for a very short time, and then quickly retiring underground. Both ants are inhabitants of the deeper, shaded woodlands, where dominant ants in general do not care to dwell. Both feed on

Myriopods or other small subterranean organisms disdained by more aggressive species. Both are perfect studies in timid conservatism, and perfect examples of the art of keeping out of the way of danger. They are rarely encountered by the higher ants about them, and they take good care to ensure this condition, walling off their chambers and galleries heavily if they happen to approach a prospective competitor. If by any chance they do wander into an optimum location, and that situation is heavily contested, they are quickly vanquished, are driven out, and soon perish. But in the more heavily wooded forests, beneath the less disturbed rocks, in the fastnesses of damp and cool soil, they have found respite from a world bewilderingly and disastrously changed since the time of their adaptable, plastic youth. They are children of yesterday, and, as such, they may be permitted to live on for some time into the future. Man himself, more than the ants, is at present acting as the agent of their destruction. For, as the forests are felled and the rocks removed, as the sun pours in on areas newly made warm and barren, the aggressive barren-ground ants follow in numbers, and quickly take over the territory from its nonplussed, shy Ponerine inhabitants, already enfeebled by the change. And so, at some time in the distant future, we may look for the disappearance of these interesting pioneers, just as the Neanderthal man eventually disappeared. But their death will be a lingering one, like that of primitive peoples, for there will for a long time be some little sanctuary left on this earth, in the undesirable portions of it, to shelter those for whom so many years ago the whole world was a heritage.

The parallel between the fates of primitive ants and of

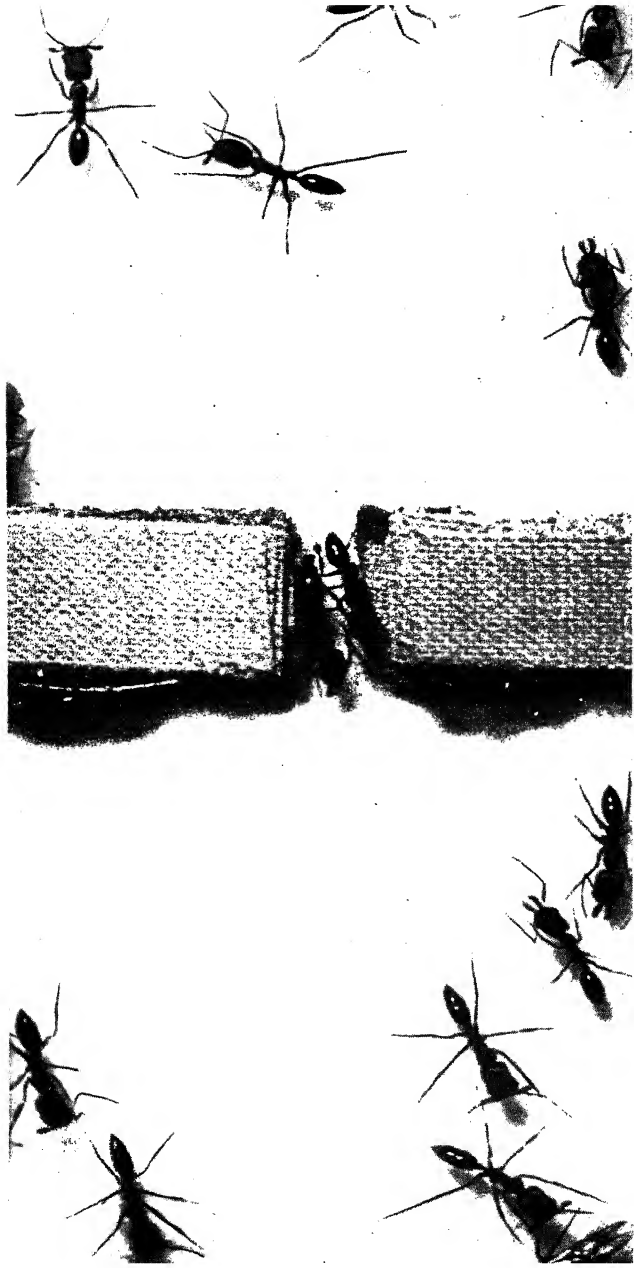
primitive men is remarkably close. It differs essentially in only one or two particulars, themselves the results of fundamental differences in the biological constitutions of ants and of men. Since all types of living men are interfertile, entirely unlike ants, hybridization offers an avenue of escape to primitive men that is entirely closed to ants. Such an escape may be an excellent one if the gap is not too wide, but very fatal in certain circumstances. One has only to consider the disastrous condition of half-caste Australians, hybrids of the primitive Arunta and Chinese or Malaysian or white groups, to realize this. Such an avenue, however, immensely accelerates the waning of a primitive people beyond that of a primitive group of ants, for a race can be exterminated no more quickly than by a group of interfertile organisms whose own traits are, on the whole, genetically dominant. Such bloodless extermination is far more rapid and complete than extinction by the sword can ever be. The other condition which has accelerated the disappearance of primitive men over that of primitive ants has been the factor of the size of men and of ants relative to the earth as a whole. It is far easier for primitive tribes of ants to find sanctuary from alien dominant tribes in hostile territory than it is for the nations of men to escape in the same fashion, for men are far more conversant with the globe as a whole than are ants. And so it is today that we are enabled to read the race-history of ants so much better than that of men, in the lives and activities of a host of living primitives, which among men long ago disappeared, never to return.

In The Future

WE COME, then, to the end of our survey of a few of the social parallels which we may discern all about us between the societies of ants and those of men. We have selected only a very few for examination, restricting ourselves to the more conspicuous and striking of the obvious parallels in the social world alone. Countless other lesser resemblances and similarities exist, quite as fraught with significance. Some of them are already known, but the descriptions of them that have been published are insufficiently detailed. We have but the merest hint of others, like the glinting tips of icebergs which give slight warning from which to guess the bulk beneath. More carefully detailed studies in the future, carried out by student or by layman—it matters not which—will give us better evidence than we have at present upon which to base far-reaching conclusions.

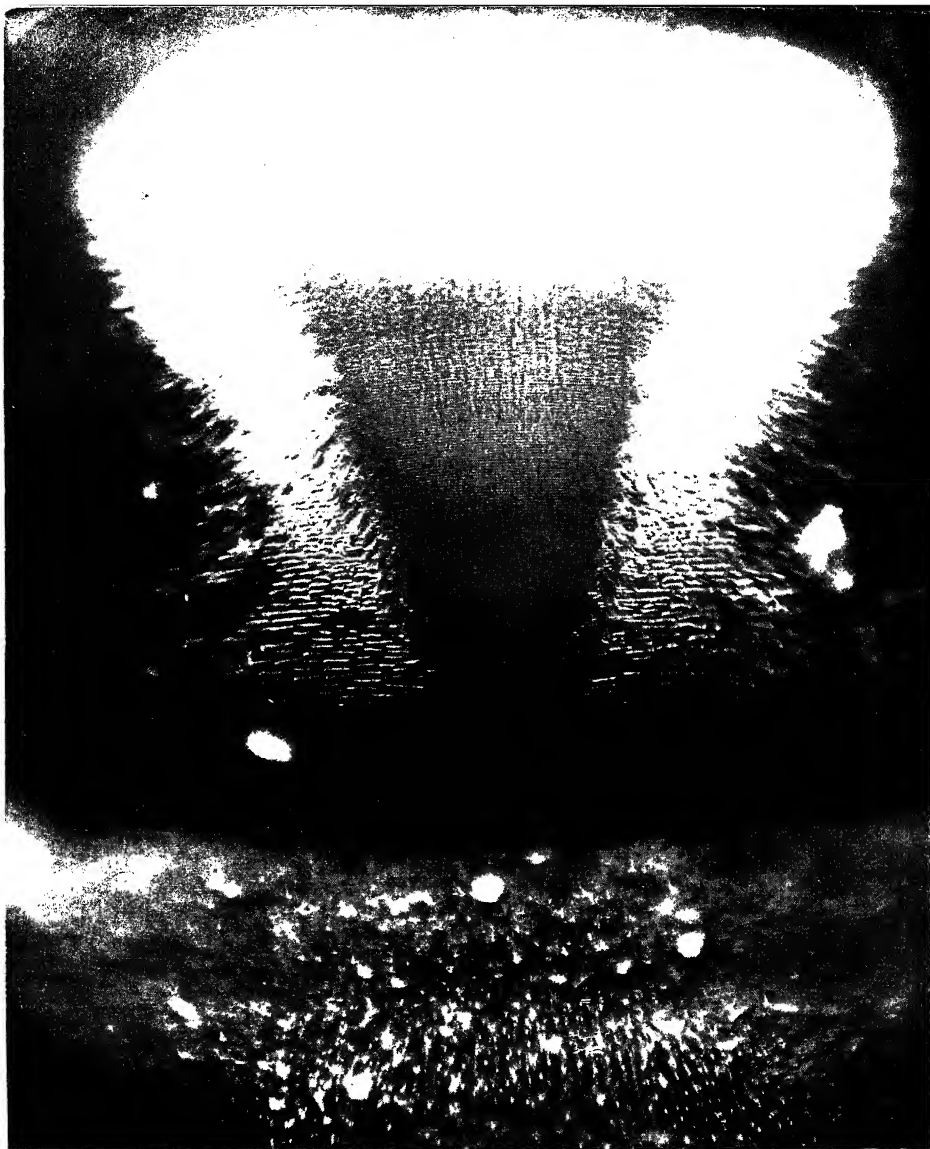
Ants seem to have arisen together with the class of mammals in Mesozoic times. It was early in these times, too, apparently, that the whole class of the termites, or

white ants, arose, splitting off as primitive social types from the cockroaches. Now the termites are as different from the ants as insects well could be. Physiologically they belong among the most primitive insects, and they can be related to the ants only through the most ancient of ties, through the stem-source of all hexapods. Yet the convergences between the social lives of termites and those of ants, evidently developed as independently as those of ants and of men, are even more striking. Both termites and ants have winged fertile forms, and both have wingless, sterile worker and soldier types. Both have an elaborate caste system among the workers and soldiers. Both live in association with other insects and both cultivate vegetable food, for there are even fungus-growing termites! The colonies of both consist of immensely enlarged families; and, as among ants, the most primitive termites live in societies of very few individuals. Both are earth-dwellers, and both live amidst a host of pets and parasites. Here again, then, are two sets of social lives which bear the imprint of a common mold. Yet they are fundamentally nearly as different as the societies of ants and men. Among the ants, as we have seen, all differentiation and social growth has been confined to one sex. Among the termites, the males and females are both differentiated. There are males and females of every caste, often very difficult to distinguish externally. There are permanent kings as well as queens in every colony. Termite young, instead of being helpless grubs like the larvæ of ants, are active little creatures, for the most part like their elders, able to run about and forage for themselves when but a few days old. No differences, surely, could be more funda-



A JUMPING PONERINE ANT

The members of the genus *Odontomachus* inadvertently jump with their long, sensitive, snapping mandibles, sometimes to the distance of a foot. The mandibles can be extended at right angles to the head, as seen in the photograph. This is one of the most "modern" types of Ponerines, and still seems to possess a degree of plastic adaptability, for it is found in the tropics around the world. The winged individuals are virgin queens. (St. George, Bermuda. *Original*.)



THE SOUND-PRODUCING ORGAN OF AN ANT

The "stridulatory file" of the Ponerine genus *Leptogenys* is unusually developed. This is a dorsal view of the portion of the third abdominal segment, which is normally telescoped under the preceding section. So perfect are these files that they function as good diffraction gratings. (*Original.*)

mental, and there is the clearest evidence that ants and termites developed wholly independently.

It is tempting, then, to speculate as to why three very different groups of creatures—the Problattids and the ants among the invertebrate insects, and the mammals, ending in man, among the vertebrates—all arising within a single great geological epoch—should all have culminated in forms which are highly social, and the general lines of whose social structures are in so many cases so strikingly convergent. What were the characteristics of Mesozoic times, from fifty to one hundred millions of years ago, which determined and foreshadowed events of this kind among its children? Or were the characteristics inherent rather in the children themselves, and was the time of their origin of secondary importance?

Speculation of this sort is most difficult and most ephemeral, unsupported as it is by information at the present day. We know two things which may be suggestive, though at best they can only dimly outline an avenue of approach to the question. We are fairly certain that mutation, or genetic change, among the creatures of the world may occur in response to the ionizing radiations which are at all times present about us, coming from the naturally radioactive substances of the earth's crust upon which we live, or entering our environment, perhaps, as cosmic rays proceeding from interstellar space, or from whatever region may at last be found to be the source of cosmic radiation. In the laboratory, X-rays, and the rays from radium and other such sources, can be made to produce these mutational changes artificially, and, moreover, they can be made to produce them at a rate which is predictable within good limits, given a knowledge of the radiation intensity. It seems most probable that this

sort of mutational change, first signalized by de Vries, has been happening among living beings throughout the ages. We are inclined to associate with it the fact of the evolution of the life of our earth as we see it today, and as it stands fossilized in the record of the rocks.

Now we of today do not feel that we can, in any way, associate evolution with progress. We have lost the cheerful feeling which once pervaded us that the end product of a line of evolution is any *better* off, in the ordinary sense of the word, than was its beginning. Wherein, for instance, is the brain cell of a genius better off than an amoeba? The brain cell can think at a rate of speed and with an intensity that would surely be inconceivable for the amoeba. But on the other hand, the brain cell can live only in the very narrowest range of environments. Remove it from the skull of the genius, let it get ever so little below blood temperature, raise it ever so little above 98°F, let its supply of food, or of oxygen, drop ever so little below the normal or rise ever so little above it, and see how quickly it collapses, while the amoeba, confronted with variations of the same order of magnitude, would quietly go about its business. It would be a bold man indeed who would say that a toucan, with his huge, unwieldy beak and his appetite for tiny berries which he must throw into the air and catch in his throat on their way down because of it, is better off than the reasonably normal barbet from which he apparently arose. It would require a bold individual to say that the immensely complex snails of Tertiary times, with their recessed, horribly rococo shells, were better off than the simpler types which have survived to our own day. Evolution, then, is not necessarily associated with progress, or with betterment. It is not, in

that sense, in any way directional. We would like to think of it so—and possibly, for the moment, in the little evolutionary sector in which our own race moves, it may be true that evolution has meant betterment. But we have only the slenderest guarantee, or even hope, that this may continue to be true for very long.

There is one factor, however, which it seems that we may safely associate with evolution as being quite invariable. Evolution, so far as we know it among living things in its ordinary sense, seems always to proceed from the simple to the more complex. The animals at the end of a line always seem to have more features by which we can characterize them than did those at the beginning. The Formicine ant shows a greater complexity of digestive system, of brain cells, of antennal structure, of castes, than the Ponerine. Man shows far more complexities of individual structure than the amœba, and so on.

Suppose, then, that we regard the process of evolution, for the moment, in this light. A simple organism undergoes a mutation, such as we can produce in the laboratory, absorbing at the same time, presumably, some radiant energy in the process. Now we find in the laboratory, and there is ample evidence in nature, that there is nothing to indicate whether this mutation shall be injurious, of indifferent value, or beneficial to the creature experiencing it. All three types of mutation must occur often, but the first two, and especially the first, are certainly the commonest, for the definition of *usefulness*, in any creature, is a narrow one, and necessarily restricts the number of random changes which can fall in that class to a very few. The creature, however, is faced with two grimly unchangeable facts. The muta-

tion, whatever it is, which has occurred without any volition or wish or desire on its part, will stick, if it be a germinal one, generation after generation, so long as the species endures, unless the very rare phenomenon of a so-called reverse mutation take place. And that creature must live, if it possibly can. If the change has been of a helpful or an indifferent character to it, the creature is not much affected. But if the change has been in the nature of a deformity, relative to its environment, the creature *must try to get into an environment where the degree of that disadvantage is as small as possible*. This it proceeds to do, and if it succeeds in reducing that disadvantage below a certain maximum, it remains with us on earth and reproduces its kind. Otherwise it perishes, and the ranks of those which have perished in this wise must surely exceed by an immense number those that have passed the hurdle.

Suppose, now, that the creature in which we are interested passes this first test and continues to live and to reproduce its kind, as a changed organism. Sooner or later, another change descends upon it from an inscrutable universe, and a readjustment must be made over again, with a corresponding change in its way of life, and the consequent failure of some of its companions. Many of these changes will be small, and the consequent adjustments will not, immediately, be either large or striking ones. But nature works upon a grand scale, through many millions of years and with many millions of living creatures. And always the ranks of the living include only those which have accepted each mutation as it came, and have built upon it a life continually tolerable. Sometimes it is better than the earlier life, sometimes worse, but always it is necessarily more com-

plex. For only in the very rarest of cases is any return road offered—a mutation once effected “sticks,” in general, for the rest of the life of the race.

It follows, then, that the greater the average number of mutations occurring in the creatures of earth per unit of time, the more rapidly will they evolve, and the more complex patterns of life will they develop. The more rapidly, too, will their ways of life change, and the wider will be the range of environments and of modes of living exploited. Both the failures and the successes will be more numerous and more conspicuous. But we shall see only one half of the picture. For striking failures and mediocre failures alike will perish and will never be preserved for us to examine, except in the fossils of titanotheres or dinosaur, of glyptodont or aberrant ant. But the successes will all be preserved, and the conspicuous ones will outrun the less brilliant in the race for existence. And so we of a later time, turning back to survey this eventful period, will say that evolution was more rapid, and that progress was much more brilliant and conspicuous, in that age. In reality we shall be surveying no more than a selected, statistical expression of the fact that mutational changes did, in fact, come at a higher rate to all creatures of the earth during those years.

We have seen, in the past pages, how highly varied may be the social life of such a creature as an ant, and how many-faceted the existence of an individual Formicine worker has become by comparison, let us say, with that of an ancient type of Ponerine. The great variability of such a social environment, with its ever changing possibilities of sanctuary to many kinds of aberrant organisms, would seem to make it an especially

good "cover" for a wide variety of mutations, which would otherwise be intolerable to the creature wearing them. How difficult would life be for the tiny, poorly armored *Iridomyrmex* as a solitary creature, compared with the life of the giant Ponerine. Yet how very successful the mere environment of social life can make this same creature! How helpless is modern Caucasian man alone in the great papyrus swamps of Equatorial Africa, in comparison to the elephant or the hippopotamus of those same swamps. Yet, protected by his social environment, how quickly can the same man drain those marshes and make from them fertile agricultural land, adjusted to his own needs, and compel the elephant and the hippo to seek other ground, if not to perish!

It is not surprising that an environment which can do so much for men—helpless creatures saddled with mutations which they neither demanded nor desired, so far as we know—should be very popular among them, or should several times have been taken up independently. And this fact enhances the reality of the parallels which we have drawn throughout the book between the social lives of ants and those of men, while emphasizing always that these developments have been arrived at convergently, and not by development from a common beginning. Men and ants have been equally helpless in the face of the environments into which they found themselves thrown. Each type, racially speaking, has found itself confronted with the problem of new mutations, acquired in ever-increasing numbers, throughout the millennia. Each of them has passed the rigid tests of continuing existence, which have been passed by relatively so few creatures throughout the history of life on the earth. And it is but natural that they have followed

roughly the same pattern in the past, and will continue to do so in the future.

What then, was so peculiar about our Mesozoic epoch, that termites, ants, and the mammals, terminating in man, should have had their nascence then? We know absolutely nothing. But we might suggest, as the ultimate of speculation, that, on the average, the ever testing mutations, physical and psychic, were occurring more rapidly then among the creatures of the earth, resulting in more continual readjustments to environments and living conditions, in a far keener struggle for survival then than at other times. We cannot know with what physical environmental features such a condition can have been associated. Presumably its basis was physical, and it is perhaps more reasonable, in the present state of our knowledge, to associate it with a greater intensity of ionizing radiations of a certain type reaching the earth during those thousands of years than at other times. In any case, it was clearly a period of rapid experiment and adjustment, with much trial and much error on the part of living creatures, with infinitely many failures and numerous successes—with a consequently intensified search for the “best ways” for a creature to live, given certain initial conditions in its problem.

It is only natural that varying classes of creatures, whose needs acutely required it, should separately “invent” the social way of living. And once they had entered this channel, there was no leaving it, save in such very rare instances as we have considered in the case of the socially parasitic ants. It is only with the greatest rarity that a social creature can ever again become soli-

tary, for society is like a protecting shield for an organism which has become individually incompetent.

In this light, ant slavery, ant warfare, ant parasitism, and the thousand and one other aberrations of structure which characterize the ant colony, take on new significance for men. We have already indicated that the worker ant may well represent a degenerate physical mutation from the queen, which can exist only in association with her. Ants, because of their greater race antiquity than that of men, have perhaps acquired more physical mutations since the inception of social life than have we, and it is to their effective social uses of them that their caste system, and the social stability consequent upon it, has been due. We have already seen that, were dwarfs and real giants more common among us than they are, they could quite as reasonably come to form a physical caste system with corresponding duties.

Mutations, however, are not confined to the physical features or the mere body cells of an organism. They can just as well affect the nervous system and the brain tissue, resulting in the initiation of new thought-habits and a "mental differentiation" of which there may be no physical indication whatever. Ants show this especially in the instinctive field. We have already mentioned the development of the "honey ants" in the Formicine genus *Myrmecocystus*. Among the callow members of the newly hatched worker and soldier generation, some individuals quite independently take to storing nourishment until their crops become incredibly distended with the volume of the ingluvial food, and they are condemned for life to the quiet business of hanging from the roofs of subterranean chambers as animated honey-pots. Individuals of both soldier and worker castes go through

this evolution. There is absolutely no physical criterion by which one may predict which individuals of a given callow brood may undertake this apparently entirely voluntary development. The mutation is a mental one purely, affecting the instincts of certain individuals, and only by their subsequent ways of life may we know them. We see the same sort of thing in the distribution of the slave-making instinct of *Formica sanguinea*. We have already seen that although, so far as we know, all young queens of *sanguinea* form their nests with the aid of kidnapped young workers of an alien species, the habit is retained among the first *sanguinea* worker generation only in certain subspecies. Among the rest, no further attention is paid to the institution of slave-making, and the colony becomes pure as soon as the first slaves perish. Often the physical differences between some of the slave-making and the non-slave-making subspecies of *sanguinea* are so minute that only a close specialist can distinguish them in this way. Yet any one of us can tell two such puzzlingly alike creatures apart if we but see them in their nests, and can watch their daily life pattern for a day or two. Once again there is evidence that mutations are progressing in the intangible spheres of the mind, exactly as they do in a physical way, to differentiate individuals in the performance of their life work that would be completely indistinguishable on a physical basis. A high rate of psychic mutation, coexisting with rapid mutation in the physical sphere, would have tended to confirm the social habit for ants, and to increase and extend continuously the complexities and variety of their societies.

It is this sort of mutation which above all distinguishes modern man, and, though we know of its existence, and

can vaguely follow some of its workings, we are extremely ignorant of its details today. And it is most important that we should know of them, for they are the basis of our social caste system, occupying exactly the same predominant part in our society as the physical mutations among ants in shaping their social groups. Modern man, like the modern ant, shows a much larger number of mutations than more ancient and primitive types. But these mutations are nearly all in the mental field, and are therefore easily passed over by the casual observer. Consider the extreme number of recently produced subspecies in *Formica sanguinea*, and compare it with the enormously conservative physical stability of *Stigmatomma pallipes*. Compare, again, the incredibly diverse thought-patterns of the individuals of the white and yellow races, taken as a whole, to the extremely stereotyped mental processes of the Australian black-fellows or the African Hottentot-bushmen as groups. Nothing is more striking than to notice the extreme faithfulness with which composite thought patterns are reproduced among peoples in roughly the same state of primitive culture the world over, or to notice the incredibly baffling complexity of these patterns among different societies of advanced peoples. As with the rapidly mutating *sanguinea*, the opportunities offered to the rapidly mutating human are great. Correspondingly, as for the *sanguinea* too, the dangers both individual and social are much enhanced. And what some of those dangers are, in greater detail than we ourselves have ever experienced them, ants, as we have seen, can help to tell us.

It is not difficult to assign a physical mutant to its own role in a specialized society. There is little that a door-

keeping *Polyrhacis* soldier can do in its colony but door-keep, little that an *Atta* minim can do but weed the fungus garden. But a mental mutant, especially an extremely recent "intellectual" one, such as occur so many times in human society, is not so easily placed. The assignment of our mental mutants, the more specialized and striking of which we are inclined to call geniuses, to the particular environments in which their mutations will work to their and to the society's best advantages is still one of our most acute social problems. We have yet far from satisfactorily solved the problem even of recognizing those mutants when they occur. So, once again, we see that our basic social problems are still essentially those of the ants, though built, withal, upon a more dynamic and infinitely subtler plane!

We have glanced at only a limited area of the social lives of ants in this book, and have said almost nothing of their lives as individuals or of the fascinating physiological and psychological problems which they present. This restriction was made because we were most interested, by our original definition, in those phases of ant society which showed the closest correspondence with phases of the social life of man. And so we have had nothing to say of many thoroughly fascinating ants whose activities are necessarily somewhat divergent in detail. We have spoken little of the details of the pastoral and agricultural societies of ants, except of the fungus growers. Little reference has been made to the stolid grain harvesters of the genus *Pogonomyrmex* in the deserts of the New World or of the genus *Messor* in the Old, whose huge communities amass so much of the fallen seed of the grains of men at harvest time that their granaries have actually been the subject of litiga-

tion, and whose immense communities rival in numbers and in stability those of the fungus growers. We have not spoken of the keepers of aphids and Coccids and tree-hoppers and butterfly larvæ and the numerous other types of ant "cattle" from which their herders—many species of ants the world over—derive a continuous supply of nutritive sweets, and whose eggs and young they harbor, store, and protect. We have made only passing reference to the hundreds of types of ant pets and guests which are more or less indifferently tolerated within the colonies, or are treated with approximately the consideration of street-pigeons in our great cities. Like street-pigeons, they are ornamental, in the sense that they seem to offer to the gustatory and other physical senses of the ants about the same degree of satisfaction that pigeons offer to our æsthetic one. Socially they are quite as harmless as pigeons, and practically as independent. It is only when the relationship becomes too intimate that the situation takes on a socially serious significance, as we have seen with *Lomechusa* and *Atemeles*.

And we have said nothing whatever of the remarkable architectural and engineering feats of the silk-building ants of the East, principally those of the genus *Ecophylla*. These creatures are dwellers of the treetops: a single large colony, especially in the species *Ecophylla smaragdina*, the famous "red ant" of India and Ceylon, often occupies an entire tree. The larvæ are here the sole agents in the actual fabrication of the nest, for it consists entirely of leaves, bound together by strands of the larval silk! Rows of workers align themselves with a military precision on the adjacent edges of two leaves, and after much persistent effort draw them together. Another set of individuals then passes down between the rows,

carrying larvæ. The head of each larva is pressed against one edge of a leaf and a thread is attached. It is then carried over by its porter to the other leaf, spinning its thread meanwhile, and a new attachment is made. And so, shuttle-wise, the larva is passed and re-passed between the leaves, until a thin web connects them, and the entire silken supply of the larva is exhausted. It is then laid again upon the brood-pile, and another substituted in its place. Ultimately, every chamber of the colony consists of leaves bound together with silken wefts, and there is often a thick webbing or mat upon the tree trunk as a whole. Eggs and larvæ are kept between the bound leaves, protected from falling by their silken walls, and within these crevices the adults spend much of their time. The larvæ of the Formicine *Æcophylla* have unusually large silk glands, even for the larvæ of Ponerine ants which traditionally spin such thick and heavy cocoons; yet long before their normal time of transformation from the larval stage, all their silk is exhausted, and the pupæ of this talented silk spinner are naked!

These are but examples of the infinite variety in the social life of ants, of which we have examined only the very few cases that seem to offer the closest correspondence to human social life and institutions. Research in the other, more bizarre, yet less-known facets of an unbelievably complex living structure will surely bring to light other mines of information to enlarge and enrich the comparative picture, and to extend further our all too limited knowledge of ant society.

Research for the future is no less needed upon phases in the communal lives of the commonest ants about us. The very fundamentals of Formicid social existence, in-

deed, are to be traced among ants no more conspicuous nor less common than the red or black ants of the flagstones of our sidewalks. What forces, for instance, lie at the base of the remarkable habit of colony recognition, which we have already touched upon? Why should every worker ant of a normal colony immediately recognize every sister as friend, and detect the intruder, be she ever so similar in physical features? We have already seen that the contact-odor or topochemical sense is probably the one predominantly involved. But does every ant of a given colony recognize every colony sister individually, or is there a sort of standard odor for each colony? Too few experiments have been performed in this fascinating field, and such as have been done give conflicting results. It is necessary only to separate a group of ants into two halves, and to maintain them wholly apart for years, to see how quickly they will become estranged from one another, and through what interesting steps of uncertainty and growing unfriendliness that estrangement will proceed. It is only necessary to give to a colony of the commonest ant young from another colony of the same species, allow the foster parents to rear them to maturity, and then introduce sisters from the original stranger colony, to see that the acceptance of some members of a community as friends does not guarantee the equal acceptance of their sisters. So the characteristics by which recognition is achieved, whatever they may be, are evidently not stereotyped throughout the colony. And yet it is immensely difficult to think of any worker in a huge *Attiine* colony, for instance, as having individually memorized the characteristics of every one of her multitudinous sisters—and indeed, she has probably had the opportunity to meet but

a small proportion of them. The answer, perhaps, is somewhere in between, and it must lie with the competent research of the future. A correct answer would be a great help in our search for an understanding and an adequate interpretation of the simplest social problems among ants.

We know pitifully little about the means of communication employed by ants. We are reasonably familiar with many of the more stereotyped signs which they use. Solicitation of food, alarm, care of the brood—all of these we know, to a degree. We are familiar, too, with the more usual modes of use of stridulation, or with the habit of many ants of knocking upon solid surfaces with their bodies, and with other apparently auditory means of communication, although we are by no means sure of the degree to which these signs are perceived or used. We know that the topochemical sense plays a dominant part in communication, as in most other colonial activities. But the results achieved are so far beyond those which we should expect by such means that we realize only too well the pitiful state of our present ignorance, and how much an adequate interpretation must lie with the research of tomorrow. When we consider the immense complexity of the raids of the driver or the slave-making ants, taking into account the enormous numbers of individuals involved and the dispatch with which the ends in view are achieved, it seems inconceivable that the processes of liaison from ant to ant should not be more complex than our present information indicates. The phenomenon is even more difficult to understand in the beautiful columns of some of those *Ponerines* which have taken up the raiding habit, such as some of the genus *Lobopelta*. Here each

ant of the compact, swiftly moving column acts much more as an independent unit. Her eyes clearly help her very much, and she is only in intermittent communicatory contact with her fellows, though each member of the group seems to stridulate continually. Yet the precision of action of the whole column, and the swiftness with which any major change of policy, such as a reversal of direction, is communicated throughout it, are astonishing, and, in detail, quite inexplicable at present.

The associative memory of ants is remarkable, as indicated by the number of alien friendships which a very young ant will make and retain throughout her life, and the complicated training behavior patterns which she can be made to learn and repeat. Yet we know essentially nothing of the degree to which this memory can be used, for no one has ever attempted to train an ant to the limit of its ability. There is also some evidence—never thoroughly tested, though testing it would be fascinating work—that among ants an associative memory-pattern may be completely erased after anesthesia, either by drugs or by cold. It is very possible that all the individuals of a northern ant colony may have to begin life anew as freshly hatched creatures, so far as their memory or their background of experience is concerned, each spring. Such a situation might well be of aid to a colony which must face new conditions with every recurrent warm season, and may thus be spared the weighty impedimenta of useless, and clinging, impressions. But we know nothing definite of ant memory patterns—a question which the simplest experiments, carefully done by a layman upon the commonest ants, could easily answer.

The question of the means by which ants foraging

above ground upon independent trails find and keep their direction, and manage to regain their own nests at nightfall, is a fascinating one upon which little research has been done. Many young ants doubtless fail on this initial test, and we have seen in earlier pages that older workers of the genus *Formica* often find their younger sisters lost or strayed and carry them home at eventide. In this independent foraging, the topochemical sense can be little help to ants, and experiments by Sir John Lubbock and others seem to show that the eyes, and especially an active notation and persistent recollection of the direction of the general light, may play an important part. But again we know all too little, and the answer must lie in the future.

Closely connected with the problem of colony recognition is that of the social training of the young adults in the colony. We have seen that most of this training must be compressed within a very few days, because of the short period of mental and physical plasticity of the young insects. But we have only the vaguest idea of the parts which the older nurses play in this process, if they take part in it at all. Clearly the instinctive endowment of the young ant stands it in wonderful stead, and, among the Ponerines, may be all that it requires. But among those types which have relatively recently taken up complex social habits of great importance to the community, it would be difficult to imagine that the young ant would be immediately and instinctively aware of all the finer details of the pattern. Studies of the social behavior of young ants of some of the higher species reared in communities of different mores when returned to their own would be of the

greatest interest here, and have hardly been undertaken. That work, too, lies all with the years ahead.

Then there are the larger questions to be solved, whose answers must come as the result of carefully organized, concerted, directional investigations, rather than as more casual chance observations. What, really, is the antiquity of the Formicidæ, and what are the finer details of the transition by which the solitary wasp-like creature became the primitive Ponerine? Just how did the inception of the pastoral and agricultural habits of life come about, and was it like that which ushered in the similar stages in mankind? How did the habit of slave-raiding first appear? What are the conditions which govern the sudden, organized appearance of an entire colony of *Formica sanguinea* or of *Polyergus* within a few moments upon the threshold of its nest, as though in response to a single command, in preparation for a concerted raid? What, similarly, are the conditions which govern the timing of the marriage flight, when, among the commoner ants, all the adult colonies of a single species over many square miles of land may release their males and young queens for flight within an hour of one another on the same day? In these two processes, slaves and workers respectively seem to take some part, for they have been seen restraining over-eager mistresses or winged forms, as the case might be, when the threatened departure of these would have taken place too early to suit the slaves or worker attendants. Are the governing conditions meteorological ones, involving humidity and temperature? This, at present, would seem most probable, but we have no certain knowledge, and the answer to that question, again, lies with the years ahead and with future workers.

Then we know nothing of the inception of the habit of social parasitism, beyond the conjectures which we have already surveyed. How, really, do the little parasitic queens secure adoption into their host colonies? If they are given safe conduct in the later stages of the institution, their existence must be highly precarious among those species where the relation is still an unstable one and where the host queen is not killed. We actually know practically nothing in detail of the process among those species where the young intruding queen is not hostile to the queen of the hosts, and where the two can live, apparently amicably, side by side for a time. And we know and understand nothing of the condition, at a later stage of the relationship, whereby intruding queens induce their host workers to assassinate the host royalty for them!

These represent but a random few of the intensely interesting problems in the social field which must await solution by the workers of years to come. Ants raise problems of physiology which are even more numerous, fascinating, and pressing, as we have already seen. Extremely little is known, for example, of the mechanism by which ordinary sexual dimorphism is achieved in the ant. We believe that males arise entirely from unfertilized eggs, although some good controversial evidence has been forthcoming. If this is true, then the nuclei of all body cells of the males presumably contain but one half the chromatin material present for the female—which may be the determining agent, though in just what way we do not know. But the fact of the production of males, and of nothing else, invariably from unfertilized eggs must be more carefully checked. The worker-like males of some of the parasitic ants, which

we have already mentioned, likewise present a grave, purely biological problem. Have they secondarily inherited some of the traits of their worker sisters? If so, how, since we would believe that at least as many have arisen from queens as among the worker personnel?

If we know little about the fundamental biological properties which govern the distinctions between queen and male, how much less we know of those which separate queens from their workers and soldiers! Among the higher ants, we are inclined to associate the small stature of the first-brood and of the minim workers with insufficient feeding. Clearly, insufficient feeding does have something to do with the case, but it is not all that is required. For minims are still produced among many populous colonies where ample food is available for the tiny young larvæ if they desired it. Ponerines, too, whose food we believe even in the first brood to be wholly self-determined by the larvæ, still show a clear distinction between queen and worker. Workers, moreover, may often be larger in stature than their own queens, especially among parasitic species, as we have seen. We may consider workers to represent recurrent mutations. If so, how can they be carried in the germ plasm of a creature, their mother, which shows none of the degenerative features? Why do we find well-marked polymorphism among the worker brood of opulent colonies, all members of which have seemingly identical opportunities for development? Why do we find the larger members of the worker series, which clearly were once present, wholly suppressed among such thief ants as *Carebara*, and only the tiny minims retained? Clearly this is not a matter of food scarcity, for the queens of the same species are immense. And

what of the "mistakes" that so often occur in the differentiation of castes—the "pseudogynes," half-queen and half-worker, which we know to occur in *Lomechusa*-parasited ant colonies; or the "gynandromorphs," half-queen and half-worker, or half-queen and half-male, or half-worker and half-male, which frequently appear? Also, what of the astonishing specializations of body form which ants present at every turn? There are extremely long and slender ants which inhabit exclusively the hollows of the thin stems of certain bushes; flat ants which frequent only the cracks of wood or boards; ants with truncated heads to stop the holes of the tree-galls which they inhabit; and so on without end.

By what means, again, is the young fertilized queen able to keep alive in her spermatheca the sperm, which she received upon her initial flight, throughout her own extremely long life? She is almost unique among living creatures in this ability. It seems reasonable to consider many of the physical and physiological anomalies among the personnel of the colony, some of which appear only at more or less characteristic periods of the colony life, to be in some measure reflections of nuclear conditions within germinal cells. May not, then, changes which take place in the nuclei of the resting cells of unused sperm within the queen play their own part in determining colony structure?

Ants present as many unique opportunities for study to the biologist, in the strange physiological situations which arise among them, as they do to the sociologist in the unique structure of their societies. The solutions of such questions as these, and of innumerable others of far-reaching significance both in relation to the life of our earth as a whole and more particularly in its especial

bearing upon the problems of mankind, must lie entirely, as we have said, with the workers of the future. The possibilities are rich, and the facility of the research is almost unparalleled in other fields. Let us hope that advantage will be taken of the situation by many future myrmecologists, general biologists, and those especially interested in the social aspects of the problems. Students and lay observers alike, in these fields and in many others, can scarcely escape an occasional sentiment of gratitude and even—anthropomorphically but genuinely—of sympathy and admiration for these our inconspicuous neighbors, the Earth Dwellers, who were present on this planet long before our coming, and who most likely will be patiently occupying their areas of open ground, and clinging for security to the deeper earthen crannies, when our race shall be no more!

Epilogue

NO STUDY CAN BE MORE FASCINATING as a recreation or hobby, more stimulating to the imagination, or more productive of new results per unit of energy spent upon it, than the study of ants. Ants exist everywhere about us, abundant in our dooryards, beneath the flags of our sidewalks, in the lone tree which relieves the cement monotony of a city street as well as in the unfettered jungles or the wide-expanded desert wastes of the world. Not only are ants numerous in species; in colonies and as individuals they are among the most abundant insects. In contrast, to many other social insects, no two colonies of ants, even though of the same species and constructed in similar situations, ever present quite the same problems. No species of ant is so common that a careful examination of its nest habitat may not reveal some condition, social or biological, which is entirely new—not only to the experience of the observer himself, but to the experience of humanity as a whole. Regardless of how limited the field of his search, the city-dwelling businessman need never fear to tread and re-tread the same ground, for in the study of ants the same ground never grows old—the ingenuity and variety of the in-

sects themselves are far too great for that! Adventures and intellectual satisfaction of a high order may be had in the course of an hour's walk and a short search of almost any ground, for rare is the spot that is so barren that it does not harbor at least one ant colony; and the more unlikely the spot, the more interesting will the ant be, since it will have had to make special adaptations to the unusual conditions imposed upon it. No more stimulating or engrossing lay occupation than a study of some phase of ant society could be suggested to a convalescent from some bodily or mental disorder consequent upon the overwrought condition that frequently accompanies the daily business or professional activities of most of us. No occupation will more effectively keep him in the open air, provide an intellectual stimulus for his ramblings, and offer an object for concentrated, whole-hearted, consuming wonder, which is the best of mental tonics. The truest sort of adventure lies at the back door of the most restricted dweller of our great cities; and the continuing mental satisfaction which will follow will be as great as that which even Africa could provide.

Finding an ant colony, with its contained earth, its queen, its brood, and all the pets, the cows, and the social parasites which happen to be in it at the time, is only the first step in the adventure of its study. Glass nests for indoor observations can be constructed in a few moments. They need not, in general, be especially adapted to the ants, since ants themselves are adaptable and will make the best of bad situations. Once installed, these colonies can be watched for days or years, at the pleasure of the observer. Their observation may be casual or concentrated. In either case the chances of achieving

the rich satisfaction which comes with the discovery of new things is present. A mere glance, coming at some critical time in the life of a colony or of an individual in it, may reveal something startlingly new. Always the thrill of discovery is present.

Ant colonies housed in artificial nests require a minimum of attention. Nearly all of the higher ants are willing to subsist on fruit or bread or food other than insects. They are equally willing to procure this food without help, carrying it within their own formicary. With conditions of humidity and temperature properly adjusted—an extremely simple task—they will remain faithful to their own formicaries for years, and can be allowed to wander at will over table tops and floors in search of food. They will carry on their colonial activities almost unimpaired by their changed surroundings.

It is not often that a man can look down, as from a lofty peak, upon the activities of a communal creature. The greatest historians and the most intrepid explorers can do this upon mankind in but a very limited way. Yet every man can witness, as from a height, the daily activities, the trials, the failures, and the greater triumphs of the city-states of the ants about us. For this power, as well as for the satisfaction which a study of their social structure can give, with its social lessons and the ever-broadening vision which it can bring, we surely owe a great debt of gratitude to these our co-dwellers upon our planet, sharers of our woods and fields and plains and of the very air that we breathe—the Earth Dwellers.

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